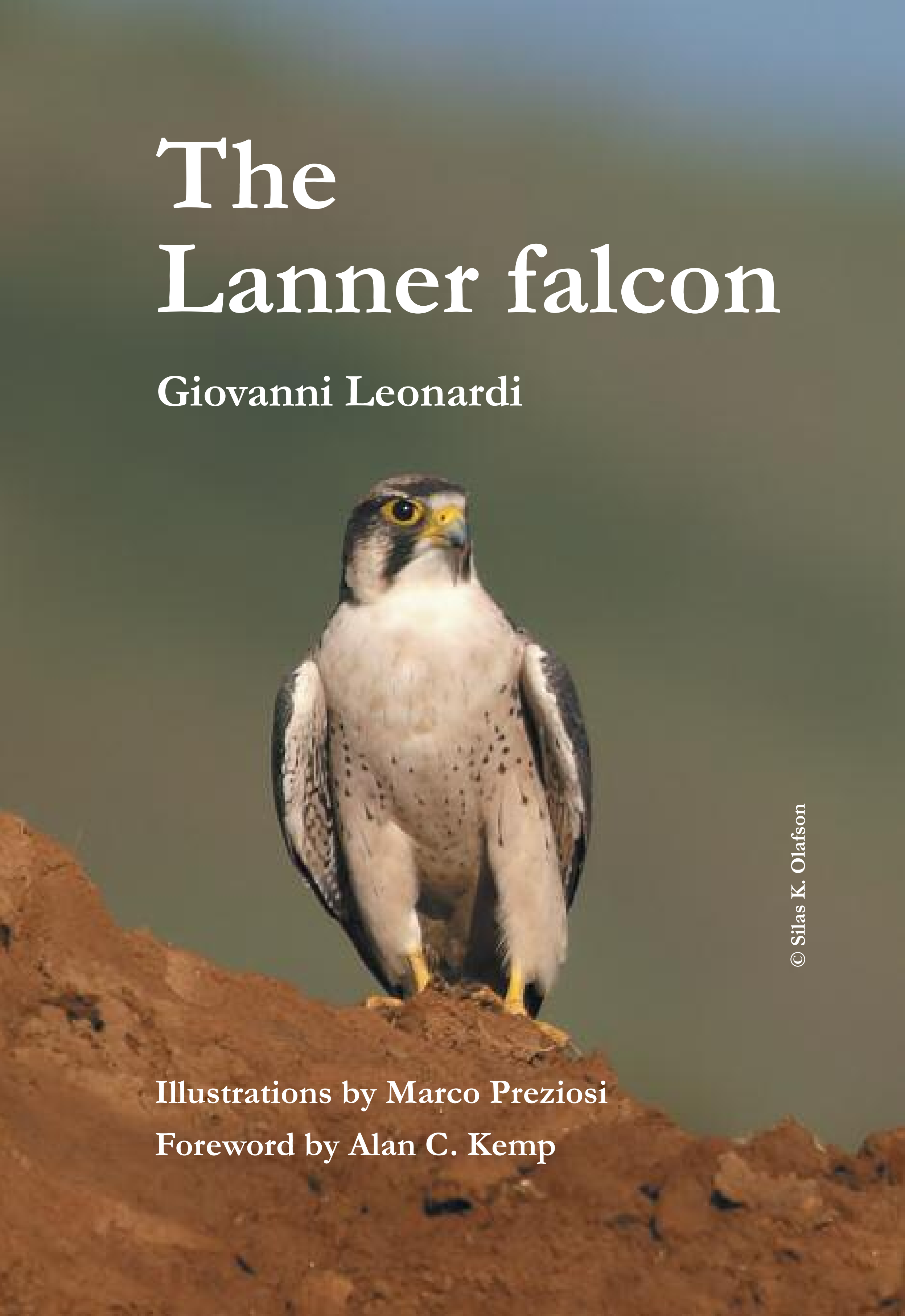
The Lanner falcon

Giovanni Leonardi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Illustrations by Marco Preziosi

Foreword by Alan C. Kemp

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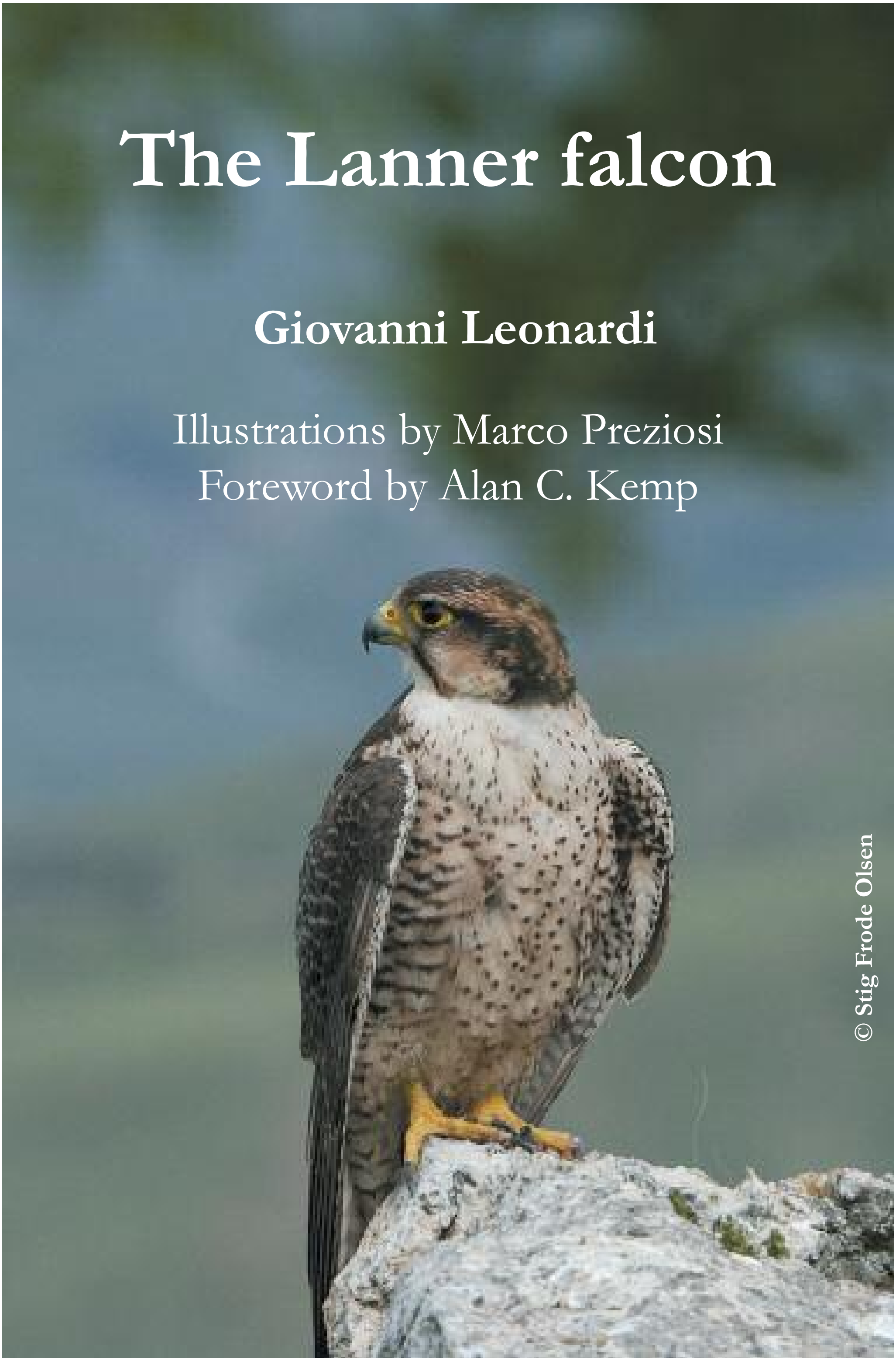

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© Giovanni Leonardi
GLE, Catania Italy
First published July 2015
Printed and bound in Italy
Revised ebook published July 2017

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At the explicit request of the author, the photographers who have contributed images have declared that all of the images published in this book have been taken without any visible impact to the behaviour or welfare of the animals, and in full compliance with the existing laws and regulations limiting access to Lanner falcon habitats and nest sites. The pictures have been carefully chosen in order to accurately depict the biology and behaviour of the species.

The photographs in Figures s12, s13, s18, 2.29 *and* 8.1 *were taken during field surveys carried out as part of the preparation of the* Italian Action Plan for the Lanner falcon *supported by the Institute for Environmental Protection and Research* (ISPRA). *Further details can be found in:*
Leonardi G., Travali S., Scrofani E., Cipriano M., Brogna A. 2007. [Protocol for the capture, handling, health and genetic monitoring of the Lanner falcon]. *Quaderni di Conservazione della Natura* 24: 85-88.

Front cover: *F. b. biarmicus* - Tanzania, © Silas K. Olofson
Back cover: *F. b. feldeggii* - Sicily, Italy, © Markus Varesvuo
Frontispiece on page 3 : *F. b. feldeggii* - Sicily, Italy, © Stig Frode Olsen

Contents

Foreword

Living in South Africa, at the southern end of its range, I think of the Lanner Falcon as **the** large falcon of Africa. Living in Italy, the author of this monograph is at the opposite and northern edge of the range of this species. There, a rather different looking large falcon exhibits the extreme form of the three other described and accepted races of the species that occur in between the two races that live around our abodes. The Lanner shares this wide range with the better studied Peregrine and Barbary falcons, highly regarded by European falconers, the Saker Falcon that just overlaps its range in the northeast, favoured by Arabian falconers, and only on the Indian subcontinent is it replaced by the rather similar Laggar falcon, least favoured by falconers.

While the Peregrine may excel in speed and rapaciousness, and the Saker in size and strength, the Lanner is probably the most adaptable falcon of them all, no slouch when it comes to hunting larger birds but not shy to subsist on small prey, even arthropods, when necessary, often hunting in tandem as pairs to increase its effectiveness. Hence it is able to thrive and nest across a wide range of habitats, from cliffs among mountain grassland or seaside forests to old stick nests in desert trees and, more recently, old wire crow nests on utility pylons or ledges on city buildings. How it has come to occupy such diverse ecosystems, adapt its plumage, diet and behaviour to each, and managed to coexist and thrive among the diverse African community of other raptorial competitors, makes for an excellent example of adaptive biology and evolution.

With this book, at last, everything that is known about 'The Lanner falcon' has been assembled in one place. The ten chapters cover the History, taxonomy and genetics; Structure and functions; Distribution and population estimates; Territory and breeding densities; Breeding seasons; Diet and hunting techniques; Movements; Conservation; and finally, a landscape-scale approach to the habitat associations of the members of the large-falcon (or *Hierofalco*) complex. The coverage ranges back in time to prehistoric fossils that occur outside the presently known range of the species, and forward to the possible options and plans for conservation of the species into the future. In between, in information-packed chapters, images and diagrams, every known detail about the species is presented in as much detail as space allows, supported by as many extracts of published and personal communications as the author can discover. The bibliography alone will make this compendium a standard reference for decades to come.

On a personal note, Giovanni Leonardi is a classic example of the saying that ? '*by your pupil you will be taught*'. When, more than twenty years ago, Giovanni contacted me about our common interest in Lanners, he was a keen young student and I a middle-aged ornithologist fortunate to have had a few opportunities to study the species. At that time, Lanners had been little studied in the wild and so my minor contributions appeared much more comprehensive than they really were. Luckily the species then fell into good hands, so that now there have been various studies of Lanners from across their range, combined into and now led by this massive compilation of all our existing knowledge. Such a life's work has the added potential of providing a strong foundation for further studies, especially by illuminating gaps in our knowledge of all that still remains to be discovered. I look forward to enjoying this important book in my retirement, and wish the author many years of enjoyment and further study on our favourite falcon species.

Alan C. Kemp

Preface

Why write a monograph on the Lanner falcon? A monograph is an attempt to collect and collate all of the available information on a species in order to present a unified overview. However, is it possible do so for the Lanner falcon? This species has always been viewed as an '*oddity*', and even the name has a contorted history, with both common and scientific names being subject to debate. Its very existence as a separate species has also been called into question and even today, as has been the case in the past, much has been written with regard to the identification of the species, its elusive behaviour, and its relationship with its main competitor, the Peregrine falcon.

Although a first edition of this book was written in 1992, and a subsequent full review written in 2001, I realized that many aspects of the biology of this falcon still remain virtually unknown. Even today this remains the biggest challenge for future research. Nevertheless, there is an enormous amount of information scattered across a myriad of publications which can add a great deal to our current knowledge of the species.

I therefore decided to collect together all of the available information in the hope of creating an overview of all that is currently known about the Lanner falcon. In compiling this information I have also referred to numerous sources originally published in the nineteenth century, as well those published more recently in the twentieth century. This has proven to be very helpful in understanding many of the anomalies that have been inherited from the past, many of which remain with us today.

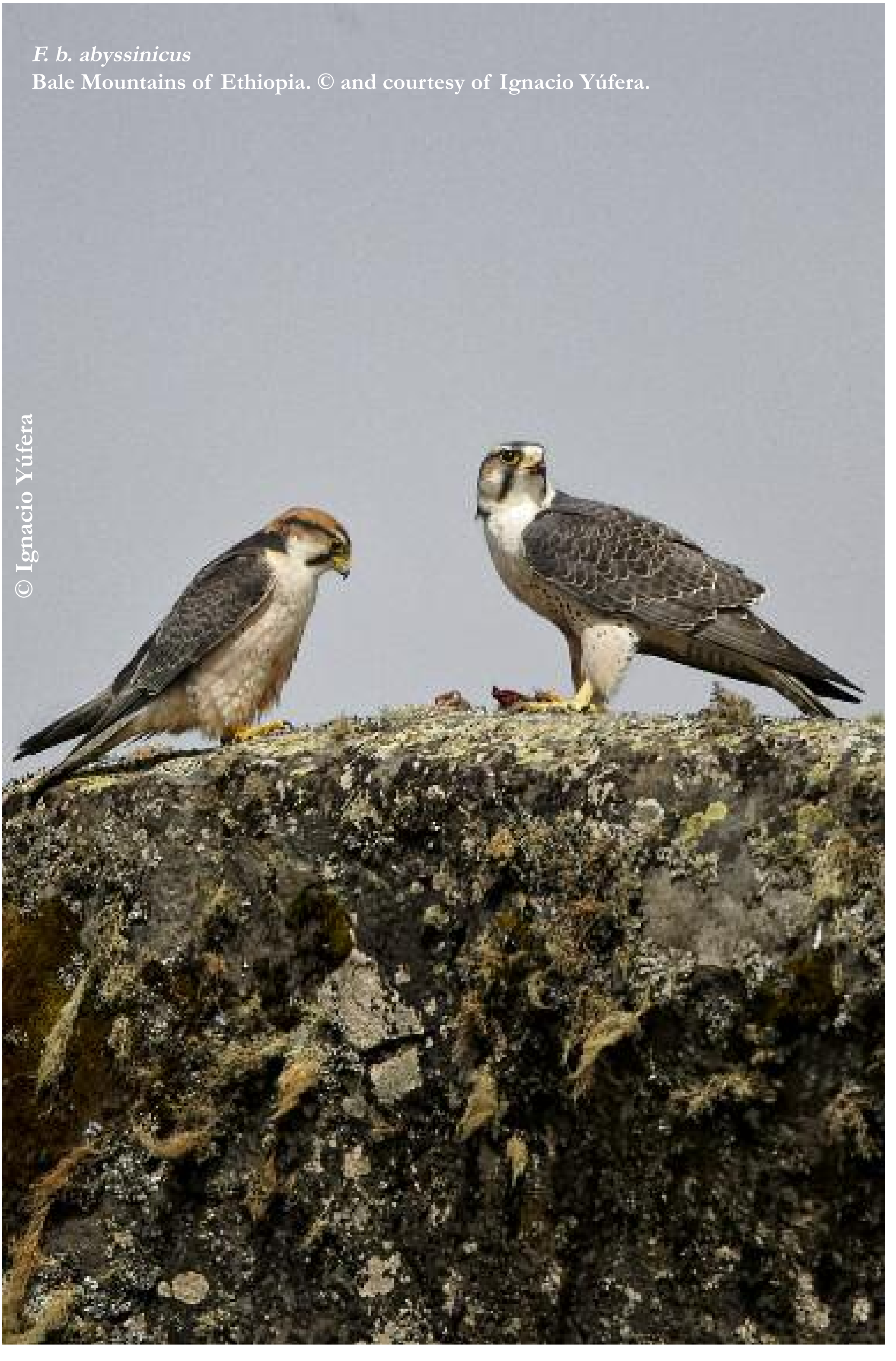
For these reasons, this monograph is not simply review of Lanner falcon biology from the many studies that have been published. It is also an attempt to create a new overview of the species that can hopefully serve as a starting point for future research.

Le ali del Lanario

Cosa scruti dalla cengia isolata
il volteggio di un sogno
incarnarsi negli artigli
discesi in picchiata
poi equilibrismi orizzontali ondulazioni
in un mare di giallo polveroso
divieni turbine di silenzio
alla tua femmina porgi
il rigogolo colto e scatti d'azzurro
baciando in un attimo
i becchi piccoli per socchiuderli
alla vita nuova dolcemente
in un tuffo che rinnova
la caccia e un altro volo
intessuto d'amore
intessuto di inviolabile

Lanner's wings

Where sweeps your gaze from the distant ledge
a dream's wheeling becomes
incarnate in your claws
plummeting down then
horizontal acrobatics undulations
in a sea of dusty yellow
now a vortex of silence
you offer your female
the oriole preyed and darts of azure
kissing in an instant
the small beaks half open
gently to the new life
in a swoop which resumes
the hunt and another flight
interwoven with love
interwoven with the inviolable



F. b. abyssinicus
Bale Mountains of Ethiopia. © and courtesy of Ignacio Yúfera.

Acknowledgements

This book could not have been prepared and published without the kind assistance of many people and institutions. Some helped me during the original draft of the first edition of this monograph in 1992 and 1993. This project was born some twenty-four years ago and many people have kindly contributed their personal field observations, publications, suggestions, and comments. I am very grateful to all of them, and I have attempted to acknowledge all of their contributions, both to the previous edition and throughout this new book.

I would like to offer special thanks to all of the photographers who permitted the use of their stunning images that greatly improve the quality of this book. A particular mention is due to Markus Varesvuo and Stig Frode Olsen for their help and assistance with fieldwork in Sicily, and to Silas K. Olofson for the front cover.

I am particularly grateful to Marco Preziosi for its amazing artwork for this book. I am also grateful to Alan Duff for reviewing the text and for his patience with irregular deadlines.

Over the course of the last twenty years this book has been greatly enhanced by my academic and field experience. For this reason, I would like to thank David Bird (McGill University, Canada) and my supervisor, colleague, and friend Alessandro Andreotti (ISPRA) whom I met during the preparation of the Italian Action Plan for the Lanner falcon. I am also grateful to all my MSc students at the Universities of Catania (M. Amato, A. Brogna, M. Cipriano, R. D'Angelo, G. Dipasquale, and A. Ossino) and Bologna (F. Nucciarone, and Lucia Goretti) as well V. Mannino for their help with fieldwork which is very much appreciated. I would also like to thank Dr. Carla Marangoni, curator of the Rome Zoological Museum, for allowing Marco Preziosi to study the specimens there while working on the illustrations. I would also like to offer my gratitude to Clayton M. White, Reuven Yosef, and Alan C. Kemp who kindly revised the manuscript of my first publication on the Lanner falcon that I wrote during the early part of my career (I still have a hard copy). This review has been a foundation for my subsequent years of analysis and fieldwork. Alan also honoured me by writing the foreword for this book.

This book is dedicated to my wife Gresy and my five year-old daughter Miriana (a strong competitor with the Lanner falcon for my time) and in memory of my father Antonino.

Chapter 1.
History, taxonomy and genetics

1.1 Fossils

The origin and evolution of the Lanner falcon *Falco biarmicus* seems to be an essential component of the *Hierofalco* (Cuvier 1817) lineage (Nittinger *et al.* 2005, 2007). Little is known about the fossil history of this group of large falcons that probably originated in Africa around the Late Pliocene, 2.5-2 million years ago (Nittinger *et al.* 2005). This so called '*cherrug*' group is relatively young in comparison to the Kestrel-like '*tinnunculus*' group, the latter represented by the *F. medius* of the late Miocene (Mlíkovský 2002). Olson (1985) suggests an African origin for the entire genus *Falco* even though the majority of living species are in South America. Unfortunately, there are only two records of *Falconidae* fossils in Africa from early Pliocene and one of these, found in the archaeological sites around Laetoli in East Africa, is closely matched to the medium-size Eleonora's falcon *F. eleonorae* (Louchart 2011).

Known fossils of Hierofalcons are mainly of Saker *F. cherrug* (Palearctic and Asia) and Gyrfalcon *F. rusticolus* (Palearctic and Nearctic), with very few known of the

FIGURE 1.1 Colossal Horus falcon wearing the double crown (Ptolemaic Horus Temple in Edfu, Egypt; © and courtesy of Giuseppina Dipasquale).

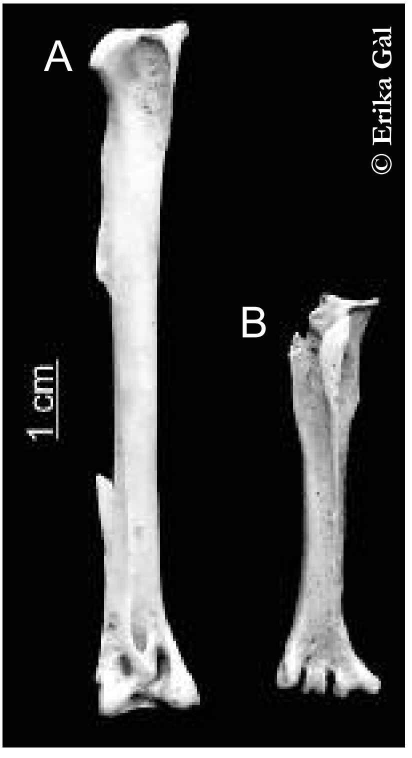


FIGURE 1.2 Medieval bones (14th century) of the Lanner falcon found in the castle area of Budapest, Hungary. A - tibiotarsus, dorsal view, B - tarsometatarsus, ventral view (© and courtesy of Erika Gàl).

Lanner (Palearctic), and none of the Laggar falcon *F. jugger* (Indian continent; Emslie 1985, Marco 2004, Nittinger *et al.* 2005, Tyrberg 2008). Table 1.1 shows fossils attributable to the Lanner falcon mainly from the Middle to Late Pleistocene (from ca. 781,000 to 11,700 years ago) and from the Holocene. Nevertheless, some doubts remains regarding the correct identification of fossilized remains attributed to Peregrine *F. peregrinus*, especially bones belonging to smaller males (see section 2.1 for details; Louchart 2002, Bedetti and Pavia 2007, 2013). Given the lack of fossil records, other evidence is needed to clearly quantify historical presence and distribution of the Lanner falcon in the Palearctic ecozone.

Sources of Lanner-like fossils are the large islands of the Mediterranean such as Corsica and Sardinia, as well as three sites in the Caucasus (Nagorno-Karabakh), Israel and South Africa respectively (Table 1.1). A large group of bones found in another site in Corsica (Coscia cave), were initially identified as Lanner falcon by Bonifay *et al.* (1998) but, after an exhaustive revision, were attributed to a new subspecies of Peregrine *F. p. cyrneus* (Louchart 2002, A. Louchart pers. comm., C. Mourer-Chauviré pers. comm.).

Fossils from Castiglione cave in Corse dated to the Middle Pleistocene consist mainly of coracoids and fibula bones of birds that lived during the early Würm glaciation (Louchart 2002). In the recent excavations at the archeological site of Ohalo 2 near the Sea of Galilee in Israel, *Falconidae* account for a significant portion (18% of skeletal elements; 17% MNI) of the bird assemblage and include also between one and two Lanner falcons (Simmons and Nadel 1998). In these areas, birds of prey were frequently exploited by man, primarily as a food source but also for the cultural and decorative value placed on their claws and feathers (Simmons and Nadel 1998). In the Eland's Bay Cave on the Atlantic seaboard of Western Cape Province, South Africa, at least two individuals (an adult and a *juvenile* bird) were discovered among three layers of materials (10-12; ca. 9.6 ka; Avery 2011). The avian fauna from these layers is mainly composed of marine (e.g. *Phalacrocorax capensis* and *Morus capensis*) and freshwater (e.g. *Phoenicopterus ruber* and *Fulica cristata*) species (Avery

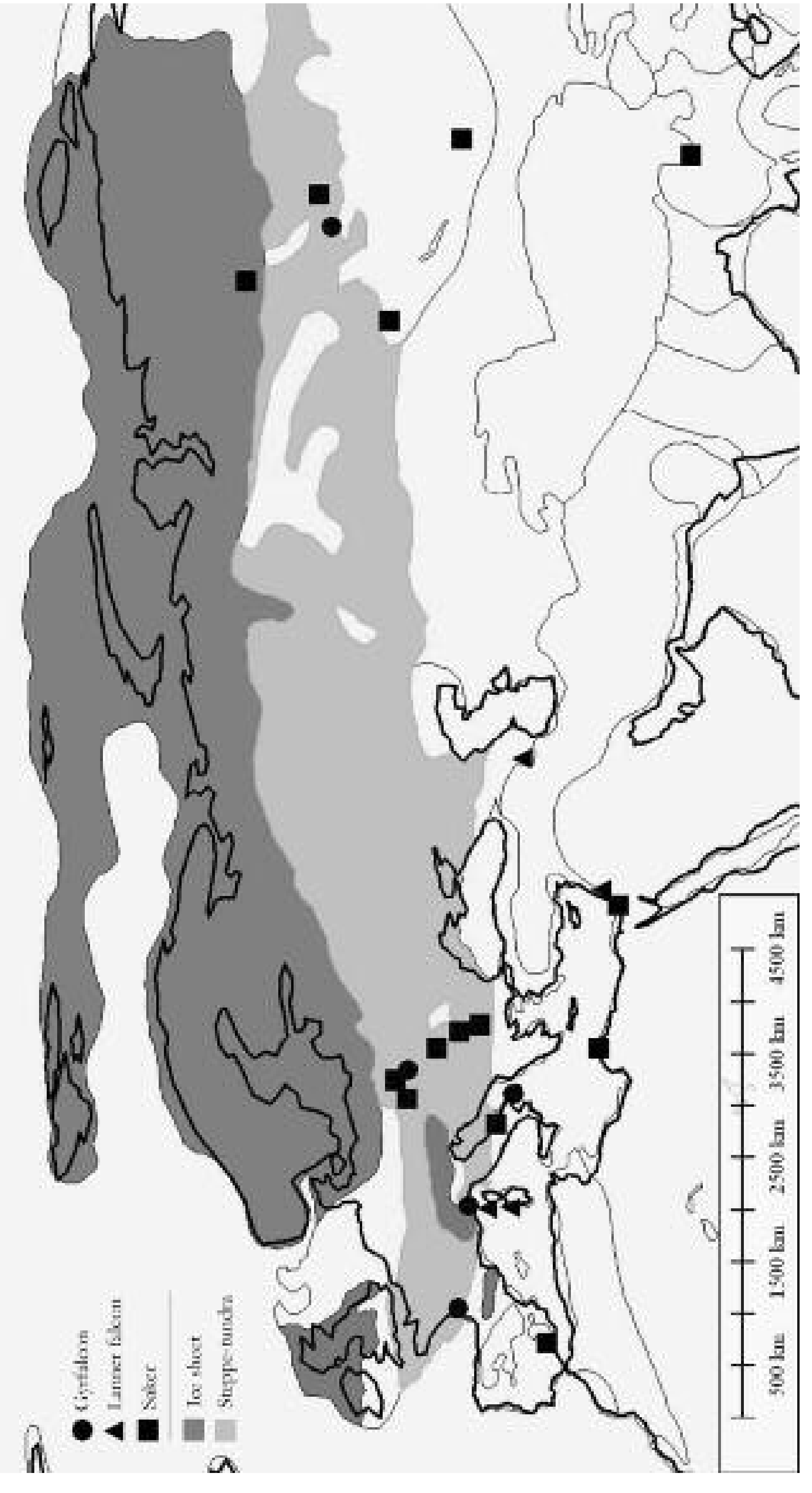
Species	Date	Site	References
F.b./F.p.	Middle Pleistocene, ca. 350 000 BP	Castiglione 3 (Corse), France	Louchart 2002
F.b.	Middle Pleistocene, Middle Acheulean, ca. 300 000 BP	Azokh, Nagorno Karabakh, Caucasus	Tyrberg 2008
F.b./F.p.	Late Pleistocene, Post-Tyrrhenian	Dragonara, Cala Calcina, Sardinia, Italy	Louchart 2002
F.b.	Late Pleistocene, Early Epipaleolithic, 19 400 BP	Ohalo 2 (Galilee), Israel	Simmons and Nadel 1998
F.b.	Holocene, Preboreal period, 9 600 BP	Eland's Bay Cave, South Africa	Avery 2011

Table 1.1 List of Lanner-like fossils from the Middle to Late Pleistocene and Holocene. *F.b.* = *F. biarmicus*, *F.p.* = *F. peregrinus*, BP = Before Present.

2011). Terrestrial birds are represented by mainly cliff breeding species such as *Corvus albicollis*, *Aquila verreauxii, Bubo africanus* as well the Lanner falcon (Avery 2011). Other finds of long bones of Lanner falcons have also been discovered dating from several more recent historical epochs including Ancient Egypt as well as the European and Islamic Middle Ages (Figure 1.2; Boessneck and von den Driesch 1989, Louchart 2002, Becker 2005, Gàl 2008).

The extinct falcon *F. antiquus*, which as been proposed as a common ancestor of Saker and Gyrfalcons, has been described in fossils dating from the late Pleistocene in southern Europe, where it is thought to have originated before expanding eastward through Asia into North America (Mourer-Chauviré 1975). Many finds demostrate relationships with prey species which could prove useful for understanding the drivers of a predator during its dispersion and differentiation processes (Dalén *et al.* 2005, Nyström *et al.* 2006). For example, there are strong and long-standing between the Gyrfalcon and its primary food sources such as the Rock Ptarmigan *Lagopus mutus* and arctic hares *Lepus* ssp. (Holder *et al.* 1999, Waltari and Cook 2005). Thus, the presumed ancestor Hierofalcon species is likely to have followed these large prey populations into new open steppe-tundra environments created by glacial retreat where fewer potential prey survived (Figure 1.3; Mourer-Chauviré 1975).

The influence of Pleistocene glaciations on species distribution would clearly less marked at low latitudes, particularly in Afrotropics, but also to some extent in the Palearctic ecozone (especially Mediterranean Europe, North Africa and the Sahara


Gyrfalcon
Lanner falcon
Saker
Ice sheet
Steppe-tundra
500 km
1500 km
2500 km
3500 km
4500 km

desert) but climatic change would still play a role. For instance, the hyper-arid Egyptian western desert, where the *F. b. tanypterus* race today breeds, was savannah grassland with shallow permanent lakes during the last interglacial period (LIG; Bocheński 1991, Tyrberg 2010). Accordingly, the composition of the fossilized avian assemblage found at Bir Tarfawi archeological site (Egypt) reveals a bulk of afrotropical species which occur together today in the Sahel savannah belt and some (e.g. *Pterocles senegallus*) that currently occur in semi-desert environment at the northern edge of the Sahara desert (Bocheński 1991, Tyrberg 2010). These same factors could also been instrumental in driving Lanner falcon populations towards restricted breeding areas in the Maghreb, Mediterranean Africa and Sahel (i.e. Mauritania, Mali, Niger; see 3.2 and Figure s23). Another hypothesis, based on the assumption that the diversification of the *Falconidae* group occurred in the Neotropics, is that one ancestral falcon species arrived from North America and colonized Eurasia and Africa (Griffiths 1999, Finlayson 2011). When climate becomes much colder during the Plio-Pleistocene glaciations, a speciation process could then occurred, driven by the geographical separation of populations, that could occasionally overlap allowing hybridization (Finlayson 2011). Diverse degrees of isolation, due to an increase in the abundance of open habitats within Tertiary forests, could have produced a change from well-defined species, such as Gyrfalcon and Saker, to analogous species, such as Laggar and Lanner falcons, and the differentiation to subspecies level seen in the African Lanner falcon populations (Finlayson 2011). As mentioned above, the small number of fossil records of the Lanner falcon does not shed any light on which mechanisms led to the current distribution of this species in the Palearctic. Additionally, the two discoveries in Sardinia and Corsica appear improbable not only due morphological features but also in relation to present distribution patterns (Leonardi 2001). In fact, there are no recent breeding records in Corsica and past observations are probably attributable to misidentification of Saker falcons (Thibauld and Bonaccorsi 1999). Similarly in Sardinia, Voous (1960) and Géroudet (1979) considered the Lanner falcon as a breeding species but confirmed sightings are exclusively of individuals outside the breeding season (Toso 1973).

Palaeo-guild of raptorial birds

The Middle and Upper Pleistocene are characterized by an abundance of diurnal

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Figure 1.3 Palearctic and Asia LGM (Last Glacial Maximum) vegetation map and spatial patterns of Pleistocene sites with fossils of Hierofalcons. Steppe-tundra was a widespread vegetation type which combined plants of both tundra and steppe ecotypes (ca. 50% ground cover by plants and the rest patchy bare). The ice sheet represents year-round ice or snow cover (Simmons and Nadel 1998, Ray and Adams 2001, Louchart 2002, Marco 2004, Bedetti and Pavia 2007, Tyrberg 2008, Bedetti and Pavia 2013).

Azykh	Castiglione 3 MP	Coscia cave	Ohalo 2
Accipitriformes	*Accipitriformes*	*Accipitriformes*	*Accipitriformes*
Gypaetus osseticus †	*Gypaetus barbatus*	*Gyps melitensis* †	*Aquila rapax*
Aegypius monachus	*Gyps melitensis* †	*Aquila* sp.	*Melierax metabates*
Aquila chrysaetos	*Aquila chrysaetos*	*Accipiter gentilis*	*Accipiter nisus*
Haliaetus albicilla	*Accipiter nisus*	*Circus* sp.	*A. gentilis*
Buteo buteo	*A. gentilis*	*Buteo rufinus*	*Circus aeruginosus*
	Circus cf. cyaneus	*B. buteo*	*C. cyaneus*
	Buteo rufinus		*Milvus migrans*
	B. buteo		*Haliaeetus albicilla*
			Buteo rufinus
			B. buteo
Falconiformes	*Falconiformes*	*Falconiformes*	*Falconiformes*
F. naumanni	*F. biarmicus/peregrinus*	*F. naumanni*	*F. tinnunculus*
F. tinnunculus		*F. tinnunculus*	*F. columbarius*
F. vespertinus		*F. vespertinus*	*F. biarmicus*
F. biarmicus		*F. subbuteo*	*F. cherrug*
		F. columbarius	
		F. biarmicus/peregrinus	
		F. peregrinus cyrneus †	

Table 1.2 Raptor palaeo-guilds found at the four archaeological sites with Lanner-like fossils (Simmons and Nadel 1998, Louchart 2002, Tyrberg 2008). The systematic subdivision is based on the recent phylogenetic analysis by Hackett *et al.* (2008) and Gill and Donsker (2013). † =extinct species.

and nocturnal birds of prey, probably due to the scarcity or absence of mammalian carnivores (Mourer-Chauviré *et al.* 2001). Nevertheless, a significant loss of species diversity, particularly among large but also small falcons, could be attributable to an increased human presence (Guerra *et al.* 2013). In general, differences in body size amongst species of predatory birds are consistent with differences in breeding strategies, prey selection and nest site selection (Smith and Murphy 1982, Poole and Bromley 1988).

In all archaeological sites with Lanner-like fossils, both large and small falcons are present as well as other large predatory species (e.g. *Aquila* sp. and *Haliaetus albicilla*) and scavengers (e.g. vultures; Table 1.2). As mentioned above, most likely the Lanner falcon never reached Sardinia and Corsica as these islands are located far from the mainland. In fact, the isolation of these two Mediterranean islands led to endemisms mainly of forest species such as the Eurasian Sparrohawk *A. n. walterstorffi*, the Northern Goshawk *A. g. arrigonii* but also of cliff breeder species including an extinct race of Peregrine *F. p. cyrneus* (Clark 1999, Thibault *et al.* 1992, Louchart 2002; Table 1.2).

Fossils of the Lanner falcon from the Middle Pleistocene discovered in the Nagorno-Karabakh region confirm the limits of the distributional range of this falcon in the Palearctic (Table 1.2; Tyrberg 2008). The recent historical observations and the last sixty years of surveys carried out in the Caucasus define the Lanner falcon as an irregular breeder with very small ephemeral demes (Abuladze 2013). These breeding pairs represents relicts, more or less stable, of *F. b. feldeggii* populations along the eastern borders not including summer nesting pairs at Lake Urmiyeh in Iran (Scott 2008, Abuladze 2013). Thus for Pleistocene period, these fossils suggest more favourable climatic and environmental conditions for the falcon species in these areas. In fact, the main glacial refuges for the Mediterranean-type plant and animal communities were in Spain, southern Italy, Sicily, southern Balkans as well as the southern Caucasus and the northern border of the Caspian Sea (Taberlet *et al.* 1997, Murray *et al.* 2010, Van der Made *et al.* 2010). These refugia supported populations of the Lesser Kestrel *F. naumanni* and the Rock Partridge *Alectoris graeca* (Tables 1.2 and 1.3). Thus, the Azokh cave, located in a strategically important route between the African and Eurasian continents during interglacial periods become a refugium in spite its high altitude (Murray *et al.* 2010, Van der Made *et al.* 2010). Following the Middle and during the Upper Pleistocene, such elevations experienced a much harsher climate that became unsuitable for the Lanner falcon as well for other species associated with a '*warm*' climate (e.g. *Stephanorhinus kirchbergensis*, *Sus scrofa* and *Panthera pardus*; Murray *et al.* 2010, Van der Made *et al.* 2010).

Conversely, the late Pleistocene climate of the Ohalo 2 archaeological site as well the region surrounding the Sea of Galilee and most of the Mediterranean was very similar to that of the present day (Simmons and Nadel 1998). In Israel, the Lanner falcon (*F. b. tanypterus*) is a rare resident species widely dispersed throughout the country with a small population also found on winter passage through western and central areas (Shirihai *et al.* 2000). Surprisingly, in the birds of prey fossils guild of the area the Saker falcon is found along with the Lanner falcon (Simmons and Nadel 1998). The Saker falcon is now a very rare passage migrant and winter visitor (Shirihai *et al.* 2000). Evidence of its presence at Ohalo 2 in these recent layers suggests the coexistence of both falcons as a breeding species, a situation that is now confined mainly to Bulgaria and Turkey. The fossil record also includes two species typical of afrotropical habitats: the Dark Chanting Goshawk *Melierax metabates* and the Tawny Eagle *A. rapax* (Simmons and Nadel 1998). At present, both species have relict populations in the western foothills of the High Atlas and anti-Atlas of Morocco. Again as suggested above, the expansion of the Sahara desert forced these afrotropical predators, including the Lanner falcon, towards more favourable areas in Northern Africa (Bocheński 1991, Tyrberg 2010).

Azykh	Castiglione 3 MP	Coscia cave	Ohalo 2
Taxa identified = 20 Prey species = 7	Taxa identified = 54 Prey species= 19	Taxa identified = 67 Prey species= 15	Taxa identified = 70 Prey species= 6
1	1	1	1
Columba livia	*Columba livia* *Pica pica* *Sturnus sp.*	*Columba livia* *Pica pica*	*Alectoris chukar*
2	2	2	2
Columba palumbus	*Merops apiaster* *Turdus sp.* *Columba palumbus* *Streptopelia turtur* *Alaudidae* sp. *Garrulus glandarius*	*Turdus sp.* *Corvus monedula* *Columba palumbus* *Melanocorypha calandra* *Calidris* sp. *Alaudidae* sp.	*Anas querquedula* *Corvus monedula*
3	3	3	3
Falco vespertinus *Falco naumanni* *Falco tinnunculus* *Buteo buteo* *Alectoris graeca*	*Buteo buteo* *Coturnix coturnix* *Streptopelia turtur* *Upupa epops* *Lullula arborea* *Anthus sp.* *Erithacus rubecula* *Corvus corone* *Serinus sp.* *Carduelis chloris*	*Buteo buteo* *Falco tinnunculus* *Falco naumanni* *Falco vespertinus* *Coturnix coturnix* *Lullula arborea* *Corvus corone*	*Falco tinnunculus* *Coturnix coturnix* *Corvus corone*

Table 1.3 Avian prey from fossilized assemblages divided by ranks of relative importance in the diet of the Lanner falcon (1 = 10 – 16%, 2 = 1 – 9%, 3 = < 1%)(Massa *et al.* 1991, Yosef 1991, Goodman and Haynes 1992, Morimando *et al.* 1997, Simmons and Nadel 1998, Louchart 2002, Grenci and Di Vittorio 2004, Tyrberg 2008, De Sanctis *et. al.* 2009).

Prey in fossil assemblages

Avian prey comprises a large part of the diet of the Lanner falcon across its whole distribution (Leonardi 2001). In at least three sites, remains of Columbiforms (i.e. *Columba* and *Streptopelia* sp.), Corvids (i.e. Jackdaws and Magpies) and larks (*Alaudidae* sp.) were found and they were probably the main prey species as in the present day (Table 1.3). Potential prey species represent between 20 to 35% of avian fossils and closely matched the diet of *F. b. feldeggii* (Table 1.3). At the Israeli site the percentage is only 8% using feeding preferences of *F. b. tanypterus* breeding in the Sede Boqer area (Table 1.3; Yosef 1991). This is probably due the past habitat composition of the Ohalo 2 site with large numbers of aquatic species (Grebes and Ducks) and very few steppe species, which are the preferred prey of the Lanner falcon in Israel, and the putative absence of pigeons and doves (Table 1.3). In fact only ten species are resident now in Ohalo 2 including the Lanner falcon and only one of its preferred prey species *A. chukar*. Despite this, it is likely that the Lanner falcon was able to exploit the marshland feeding on wader species such as *Scolopacidae* and *Charadriiade* species which are preferred prey for *F. b. erlangeri* in Banc d'Arguin and *F. b. biarmicus* in South Africa (Bijlsma 1990, Jenkins and Avery 1999).

1.2 Ancient history and Middle Ages[1]

Early attitudes of humans towards birds of prey in general, and falcons in particular, were often of a religious and animistic nature. The ancient Egyptians associated certain bird species with religious functions in grave goods and in votive offerings (Morgan and McGovern-Kreigh 2011). For instance, the mummified bodies of Lanner falcons were discovered in the Sacred Animal Necropolis at Saqqara along with some of smaller falcons such as Common and Lesser kestrels, as well as the Barbary falcon *F. pelegrinoides* (Houlinan and Goodman 1986, Russell *et al.* 1997). The ancient Egyptians clearly recognized differences among hawks, and small and large falcons specifically represented (Kozloff 2012). The pharaoh ordered the installation of sacred bird cemetery and, as reported by Herodotus, he decreed the death penalty for any-

Gallery	Age class	NI/MNI	F%
D	Adult	1	0.002
C, branch C-C	Adult	2	0.008
C, C-4	Adult	3	0.02
C, branch C-A	Adult	4	0.005
B, B-A 22/24	-	7	0.05
B, branch B-E	Adult	3	0.003
		20	**0.005**

Table 1.4 Lanners found in the galleries of Tuna el-Gebel necropolis. NMI (Min.number of individuals), NI (real number of individuals), F% (percentage of frequency). Gallery D is the oldest part and dates to the Saitic period (672-525 BC), gallery C-C was created under Ptolemy I before 304 BC, and further extensions and new subterranean passages (B and B-E) were ordered by Ptolemy II and Ptolemy III (246-221 BC; Driesch *et al.* 2006).

[1] The bibliographic research for this section and the subsequent 1.3 was mainly conducted at the Macdonald Campus Library and the Islamic Studies Library of McGill University in Montreal, Canada. Additional information came from the Biodiversity Heritage Library open access database (http://biodiversitylibrary.org/). Rozenn Bailleul Le-Suer of the Oriental Institute of Chicago provided help and further references for the section regarding the Ancient Egypt and Maura Andreoni for the section dealing with the Graeco-Roman period.

body who mistreated or killed these revered birds (Driesch *et al.* 2006). In the Valley of the Queen in western Thebes, tomb number ten contained at least 280 Sacred Ibis *Threskiornis aethiopica* as well as 23 separate species of diurnal birds of prey including a mummified male Lanner falcon (Ulna - length 87.2 mm; Distal width 9.5 mm; Boessneck and von den Driesch 1989).

In the subterranean animal necropolis at Tuna el-Gebel (Middle Egypt), an initial survey revealed at least 3,744 birds, mainly Sacred and Glossy ibises *Plegadis falcinellus* but also twenty Lanner falcons (Table 1.4; Driesch *et al.* 2006). Different kind of jars were filled with bones of individual birds heavily soaked with turpentine, and with mummies shaped in the form of a falcon-headed god (Figure 1.4; *Osiris-Horus-Falcon*; Driesch *et al.* 2006). Major raptor assemblages were found near the entrances of the Ptolemaic decorated baboon chamber (C-4, chapel of Thot) and chamber B-A 22/24 (chamber of Teephibis; Table 1.4; Driesch *et al.* 2006). In these ancient complexes, falcons were treated and mummified by cultic servants that managed the money and inscriptions of devotees of Horus and Osiris worship (Russell *et al.* 1997, Driesch *et al.* 2006, Morgan and McGovern-Kreigh 2011). Usually Horus (*Har-si-ese*), son of Osiris and god of the sky, is portrayed as a falcon or a falcon-headed man wearing a double crown, symbol of kingship over the entire kingdom of Egypt (Figure 1.1; Wilkinson 2003). In addition, Horus is recorded in Egyptian hieroglyphs as *ḥr.w* (pronunciation **Ḥāru*) meaning *falcon* (Meltzer 2002). Horus (literally *the one who is far away*) is also associated with a mythological transformation into a falcon with theological implications

Figure 1.4 Unwrapped falcon mummy of the Oriental Institute Museum collection (© and courtesy of the Oriental Institute of the University of Chicago, photo Anna Ressman).

regarding the transfer between the earth and sky (Driesch *et al.* 2006, Scalf 2012). Since ancient Predynastic times, Horus depictions remained unchanged for two millennia and focused on symbolic and decorative qualities and not on associations with wild birds (Houlinan and Goodman 1986, Podgórski 2010, Porter 2011). It is possible that the Lanner falcon may also have been used as a model for the transfiguration of Horus (Podgórski 2010, Porter 2011, Kozloff 2012). The strong relationship with this deity also influenced John Gardner Wilkinson, '*the father of British Egyptology*', who coined the name *F. aroeris* for the sacred falcon of the ancient Egyptians (Wilkinson 1878). Adams (1894) identified the *aroeris* as the Common Kestrel due the high numbers of mummified individuals but Gurney (1876) argued that the description given by Wilkinson more closely matched the Lanner falcon. Recently, Kozloff (2012) proposed the Lanner falcon as the sole model for Horus representations based on morphological and behavioural traits. On the other hand, Porter (2011) states that the Peregrine and the Common Kestrel can be most clearly identified in Egyptian art and the Lanner falcon detected only in some of the facial and head features (i.e. the bold black hook at check back). Undoubtedly, the Common Kestrel appears in Sennedjem's and Nefertari's tomb paintings but the beautiful painted stone inside the Mortuary Temple Hatshepsut at Deir el-Bahari may not be attributable to a single species such as the Peregrine (Houlinan and Goodman 1986, Porter 2011). Adams wrote in 1894: '*There are several large moustached Falcons among the hieroglyphic writings, and also on the walls of the temples and tombs; but all are so extravagantly coloured that there is no possibility of making out the species*'. For the Egyptians, depictions of birds where the tail is dominated by green, the top of the head and neck mainly blue and wings with blue spots on greenish feathers are colour combinations with great magical significance (Podgórski 2010). Despite this, Egyptian artists demonstrate an in-depth familiarity with many bird species, and many are depicted accurately enough to permit an identification to species level (Wyatt 2012). Millions of birds where handled, treated and buried for several cults and, after Ibises and the Common Kestrel, the Lanner falcon is the third most frequently mummified bird, both in the Upper and Lower Egypt (Driesch *et al.* 2006, Podgórski 2010, Ikram 2012). In some cases, a Horus silhouette representing deity focus on some specific traits such as black moustache, the tooth of the bill and the large round black eye that allows identification to a falcon *sensu lato* (Porter 2011). More prosaically, as reported by Antinori (1864) during his sojourn in Egypt, this relationship continued to be popular into the modern era where a dealer in Cairo named a naturalized Lanner specimen as '*F. horus* Heuglin' for tourists (actually, Heuglin -1856- described *F. horus* as the Sooty falcon *F. concolor*).

Many Greek and Latin Authors from Aristotle in the fourth century BC to Plinius the Elder in the first century AD, through to C. Aelianus in the second and third century AD and St. Isidore of Seville in the seventh century AD mention many species of raptors including falcons, generically called by the Latins *accipitres* (derived from the verb *accipio*, from *ad* 'towards' and *capiō* 'take'; Is. Ethym. VII, 55) or *falcones* (see 1.3). These ancient Authors mention the use of *accipitres* in divination and falconry (Plin. Nat. Hist. X, 10; Ael. Nat. An. II, 42), but often it is hard to recognize the species that are being referred to as different names are often used for the same birds and these names sometimes do not correspond to the aristotelic descriptions (Plin. Nat. Hist. X 9, 10, 69, 95; Arist. Hist. An. IX, 36, 620a; see Epstein 1943 for a review). In augury, the divinatory practice of interpreting omens by observing birds, falcons were included among the *alites* (Cic. Div. II.34), which gave omens by their flight offering either a favourable auspice (*auspicium ratum*) or an unfavourable one, depending on which side of the Augur's designated area they appeared on (Plaut. Asin. II.1.12; Cic. Div. I.39). Beginning in the second and the third century AD, Roman mosaics often illustrate the activities of hunts with depictions of hunting dogs and falcons. Some of these have survived from Carthage and El Djem in the present-day Tunisia, but one of the most beautiful is the floor mosaic of one of the smaller rooms of *Villa del Casale* in Piazza Armerina in Sicily, dating from the fourth century AD which depicts the kinds of hunts which probably occurred in the vicinity of the *villa* such as boar hunts, hare hunts, stags driven into a net, and bird hunts with falcons. Another significant example is the falcon hunt mosaic from the Villa of the Falconer in Argos dating from the sixth century AD, where a falcon can be seen snatching up a fleeing rabbit while another scurries for cover. The Lanner falcon does not, however, seems to be recognizable in any of these ancient mosaics (Åkerström-Hougen 1974).

Laws, written in the eighth century, classified falcon species into three types: *chranohari* (crane hunter), *canshapuh* (geese hunter) and *anotaputh* (duck hunter), the latter being the *Faucon Lanier* of the medieval French falconers (see 1.3; Neyrod 2004). In this post-Roman period, falconry flourished in Europe and the Saxons and Normans turned it into a sport of kings, although falconry earns a place in all levels of society. At the beginning of the eleventh century, we can find Arab falconers such as Guillelmus falconarius who teaches and practices falconry at the court of King Roger of Sicily also using *falchonem laynerium* (Evans 1967, Battaglia 1977, Masseti 2009). The *Galeran de Bretagne* (ca. 1212), a French romance by Jean Renart, describes several species of trained raptors including Gyrfalcon, Goshawk, Sparrowhawk and Peregrine as well as the Lanner falcons (Evans 1967). Giraldus Sylvester (d. 1220) mentions a falcon with a French common name rendered in Latin as *Lanerius* a term also used by Daude de Pradas and Bertran de Born (ca. 1220), two of the most famous troubadours of the time (*Faucon lainier*; Lindfors-Nordin and Gamillscheg 1937).

In the fourteenth century, Petrus Crescentius was asked to write a treatise on falconry by Charles II, King of Sicily (Oggins 1993). During the same period, a School of Translation in Palermo (Sicily) obtained a great deal of information on falconry from Arabic sources (Battaglia 1977). According to Masseti (2009), in the Middle Ages the falcon is the quintessential figurative symbol of both the Muslim emir and the Christian prince. In fact, falconry connected the medieval elite of western Christianity and the Islamic world, influenced by the Persians, with the Umayyad and Abbasid courts, and ultimately Christian Europe (Martinez Enamorado 2011). Around 1240-1241, Frederick II of Hohenstaufen (1194-1250) could benefit from these extensive translations (so called *Falkenbuch*). Among others, he commissioned a Latin translation of treatises written by the famous Arab 'Authors' *Moamin*, *Adham* and the Persian *Ghitrīf* expressly for the Hohenstaufen dynasty (Battaglia 1977, Allen 1980, Oggins 1993, Martinez Enamorado 2011). Unfortunately, the first treatise written by Muhammad ibn 'Abd Allāh al-Bāzyār is not preserved today in its entirety but is known only through extensive excerpts cited simply as *al-Mutawakkilī* (dedicated to the Abbasid Caliph al-Mutawakkil) that formed the basis of the major portion of a Latin compilation known as *Moamin*, a corruption of the phrase *amīr al-mu'minin* meaning '*prince of the believers*' (Tilander 1943, Akasoy and Georges 2005, Martinez Enamorado 2011). Theodore of Antioch, a Syrian doctor and scientist, was responsible for the translation of this book, and even the emperor himself assisted with several corrections to the drafting of the Latin version (Trombetti Budriesi 2000). In this book, the Lanner falcon was described as the third falcon used

A	B
Au biau **faucon lanier** *mauves* *Resamble maint homme de fès. (...)* *Quant les perdris sont en seson* *Et on le gete pour voler,* *Sachiez que il ne veut aler:* *A la terre s'assiet tant ost* *Jusqu'atant qu'il trueve qui l'ost* *Son mengier veut avoir por nient* *Par la mauvestié qui le tient*	*Or torna 'n tuo paese,* *E sie prode, e cortese:* *Non sie* **lanier**, *nè molle,* *Nè corrente, nè folle.* **C** *Pompeo dipinto co' suoi cavalieri* *èvi, come vi trasse in grande fiotta;* *e disse ai suoi: «Or non siate* **lanieri**; *entrate in mezzo tra loro e la rotta»* *ch'iera nel muro.*

D

Il n'y avoit si hardi Sarrazin qui l'osast oncques attendre, mais
fuirent devant luy comme fuyt la perdis devant le **lanier**

Table 1.5 *Dit du faucon lanier* (A), an excerpt (B) from *Il Tesoretto* (1260-1266) and an excerpt (C) from *L'Intelligenza* (Dino Compagni ?, early 14th century) where *lanier*/*laniere* is a synonym of coward. Conversely, from an excerpt (D) of the prose version of *Mélusine* (1478), the *lanier* scared the *perdis* (cf. partridge; Comfort 1920).

in falconry after the Gyrfalcon and the Peregrine as follows: '*The third falcon is called anyclen* (cf. Lanner; see 1.3)*, a slender falcon used in Greece and Syria able to catch lesser prey than the Peregrine'* (Tjerneld 1945). The last *falkenbuch* named *Ghitrīf* was written by the Master of the Hunt of Hisham and al-Walid II caliphs (724-744 AD) al-Ghitrif ibn Qudamah al-Ghassani a falconer (*al-bazyar*) who introduced new ideas and techniques from Persia (Allen 1980).

This extensive background information obtained from Persia and Islām world by Frederick, as well as extensive practical experience with falcons, emerge from the chapters of the famous *De Arte Venandi Cum Avibus* (Pal. lat. 1071; Biblioteca Apostolica Vaticana; permanent link http://digi.vatlib.it/view/bav_pal_lat_1071/0001), an early compilation of text on falconry written in Latin and cited extensively in subsequent treatises (Oggins 1993). The so-called *desert falcons* were introduced into Europe by Crusaders who returned home from Palestine, as well from Maghreb to France (Wood and Fyfe 1943, Viré 1966). These birds of open lands were able to live on a coarser diet than other species used for falconry but had a reputation for tending towards lethargy (Allen 1980). Frederick II also probably brought Lanner falcons from the Middle East but, as documented, he sent his falconers, such as Stefano Mustaccius, to collect birds particularly in Sicily and the surrounding small islands but also in Malta (Bresc 1980). Also in Sicily, there was an extensive exchange of information with Arab falconers, particularly around the latest training techniques and the use of hoods for falcons which was pioneered in Eastern Islām (Allen 1980, Oggins 1993). It appears that four species of falcon were recognised: *girofalcones*, *falcones sacrii*, *falcones peregrini* and *falcones lanerii* (or *laynerii*) and sometimes the adjective *vero*, or '*true*', was inserted before both *sacrii* and *lanerii* (Yapp 1982). Frederick greatly admired the Lanner falcon despite its smaller, more slight body compared to the other species. In fact he wrote: '*However, one cannot judge these falcons by their form or by their feathers alone; we regard as most beautiful those that in all respects resemble the Saker* '(Wood and Fyfe 1943). On the subject of the poor hunting abilities of the Lanner falcon when used for falconry, he wrote: '*both falcons readily become cowards, but the Lanner has less courage than the Saker and therefore requires more exercise and training. The former does not perform various manoeuvres in flight at herons as vigorously and boldly as the Saker'* (Wood and Fyfe 1943). This opinion was shared by French, German and Italian poets who used the word *Lanier* in their lyrics as a synonym of coward (Table 1.5 B, C). Around the end of 1188, Gerald of Wales also associate this falcon species with the bad trait of cowardice: '*Falcones Hibernia praeter generosos non habet. Desunt enim degeneres illi, quos vulgari vocabulo Lanerios vocant'* (Evans 1967). The minstrel and poet Badouin de Condé (d. 1272) also made a disparaging comparison between the Lanner falcon and other raptors which were more capable of pursuing large prey (Abeele 1990). In the same way, the thirteenth century poem entitled *Dit du faucon lanier* described, through comparison with the bad qualities of the Lanner falcon, a lazy and poor man (Table 1.5

A; Abeele 1990). Brunetto Latini (c. 1220–1294), an Italian philosopher and scholar, in his *Il Tesoretto* (The Little Treasure) in Italian verse, extols the virtue of bravery and encourages readers not to behave in the same way as a *Lanier* (Table 1.5 B). In the French book *Le livre du faulcon* or *Le Livre du faulcon des dames and Faulcon damours* (ca. 1500), an allegory in poetry and prose, the Lanner is also associated with jealousy with aiming to separate lovers (Harting 1841). In German poetry, the term *blā-vuoz* (blue legs) replaced *lanier* but had many of the same associations (Dalby 1965). For instance in a verse poem, Queen Modassine dissuaded her husband the King of Greece from attacking Demantin even though his troops outnumbered the enemy since his soldiers behave as poor quality *blā-vuoz* falcons (Dalby 1965). On the other hand, the *Kitāb al-Bayzara* (385-995 AD) written for the Fatimid caliph al-Azīz bi-llāh is in complete disagreement with the falconry practiced in Eastern Islām in that it does not associate the Lanner falcon with a supposed lack of courage (Viré 1966). As support, this book listed some of the prey that could be hunted by trained Lanner falcons such as the European Stone-Curlew *Burhinus oedicnemus*, the Houbara Bustard *Chlamydotis undulata*, *Corvus* sp., *Lepus* sp., the Great Bustard *Otis tarda* and the Barbary Partridge *Alectoris barbara* (Viré 1966).

As to the distribution and breeding habits of the Lanner falcon, Frederick II says *'Lanner falcons* (Laynerii) *breed in all climates and lands mentioned above* (cf. northern Europe)*, as do other falcons. They have arboreal nests in those countries where the Saker falcon breeds'* (Wood and Fyfe 1943). Based on this erroneous assessment of the breeding range, Yapp (1983) suggests that Frederick II uses the names *Layner* and *Sacer* as merely variants of the Peregrine falcon. The illustration at the foot of Folio 56*verso* of the book *De laneriis* shows five birds, none of which has the diagnostic rufous crown of the modern Lanner falcon (Yapp 1983). The illustration on Folio 67 of a large falcon hunting small mammals and lizards also does not resemble a Lanner falcon (Yapp 1983). On the other hand, a falcon with a almost chestnut crown portrayed on folio 55 does resemble a Lanner falcon but the text description identifies it as a Peregrine falcon (Yapp 1983). Nevertheless, the illustrations in *De Arte Venandi cum Avibus* are somewhat less detailed by Medieval standards and may have suffered from a lack of personal supervision by Frederick II who died before its publication (Yapp 1983).

Albertus Magnus (Albert the Great, 1193/1206-1280), a Catholic saint and mentor of Thomas Aquinas, in his Latin treatise *De falconibus* (written around 1250 and later inserted in the larger work *De Animalibus*) described among less noble falcons (*ignobilium genera*) three varieties of *Lanarius* divided by colours: white, black and red (Smets 2002). These different feather colours were thought to reflect the dispositions of each species of falcon as suggested by Guillelmus falconarius and Dancus Rex. So black feathers were associated with melancholy, white feathers with a phlegmatic disposition and red with a sanguine temperament (Oggins 1993). Albertus however also described buzzards (*Buteo* sp.) and kestrels as *Lanarius* (Schmidt 1909, Lindfors-Nordin and Gamillscheg 1937, Dalby 1965). Arabic medieval treatises also had nick-names for raptors that were linked to colours such as *saqāwā nahlī* (honey-coloured lanner), *abū l-ahmar* (redhead) and *saqāwā aswad* (black lanner) as well as the Sooty falcon and the Eleonora's falcon (Viré 1977). Albertus wrote in the encyclopaedist tradition basing much of his work on earlier writers, especially Frederick II and William the falconer of King Roger, but with a new scientific approach that employs morphological and behavioural traits for falcon classification (Oggins 1993). For these reasons several attempts have been made to accurately identify the species of falcons and hawks that he described (Thienemann 1846, Lindner 1962). For example, Thienemann (1846) proposed a new species called *F. rubeus* based on the descriptions of Albertus Magnus that included specimens belonging to all Lanner falcon subspecies from Dalmatia, Greece, Egypt, Tunisia and the Cape Province in South Africa (Mlíkovský 2005a).

Another problematic taxonomic relationship concern falcons which are described as '*qui habet pedes azurinos*' (which have blue legs) and which Lindner (1962) considered to be without doubt to be a reference to Lanner falcons (see below for details). Along with other species of falcons (*nebli*, *bahari*, *sacer*), the Lanner (*borni*) is also mentioned in the ordinances of King Alfonso X (thirteenth century) along with several criteria (i.e. age, size and quality) for the setting prices of these birds for falconry use (Neyrod 2004). Abū al-Hasan Alī al-Mas ūdī, a Arabian historian and geographer of the tenth century, in his book *Muruj al-dhahab* (Meadows of Gold) wrote extensively on falconry and the different species of falcons used for it (Lewicka-Rajewska 1997). However, as with other Eastern Islamic sources, the main species mentioned are the Gyrfalcon, the Peregrine and the Saker falcon (see 1.3; Viré 1977). This is somewhat surprising given that other field notes written by Arab scientists show a remarkably in-depth knowledge of the Lanner falcon as a species, both in terms of identification and habits. In 1371, Muhammad Ibn Manglî (Viré 1984), in discussing the status of Saker and Lanner falcons in Syria and Egypt, wrote: '*The true Saqāwā* (cf. Lanner) *is a rare species that occupies steppe areas and uneven terrain. Scientists and experts distinguish this species from the Saker and the Peregrine*'. He adds that '*Persians call it Tcharkh Châhâin which means -Saker close to Peregrine*'. Finally, he gave a fine description of the migratory behaviour of this species in the Middle East: '*One can occasionally encounter this falcon in this country* (cf. Egypt) *during its passage off the coast*'. Likewise Abd al-Rahman ibn Muhammad Al-Baladī in his *Kitāb al-kāfī fī al-bayzarah* explains that the male of this falcon is called *saqāwah* (pl. *saqāwat*), is often confused with the Saker, and is found in Syria as well as in Hijāz in the north-western region of the Arabian Peninsula (Shehada 2012). In fact in Syria, bones probably identifiable as belonging to a Lanner falcon were found inside the Great Mosque in the centre of the early Islamic city of ar-Rāfiqa in the middle of the eleventh century (Becker

2005). The Lanner falcon is also noted by Arabic texts to be a bird to fly at the Partridge (*Alectoris* sp.), *Corvus* sp., Magpie (*Pica pica*) and the European Stone-Curlew which are all described as prey belonging to the art of *Basse volerie* or low flight falconry (Bree 1859, Allen 1980, Fenech 2010). Nevertheless, both Frederick II and Arab falconers loved the Lanner falcon for its plumage, especially the pale rufous and cream nape, and included it inside a cadet branch of a noble family (Whitaker 1905, Allen 1980). In the hierarchical medieval society, the Lanner falcon was a prerogative of the esquires practicing falconry, after the Saker which could be used by knights and before the Merlin (*F. colombarius*) used by ladies (Schelgel and Verster de Wulverhost 1845, Oggins 1989). These *Ladies Hawks* used frequently Lanner falcon males, referred to as *Lanneret*, and described by François Rabelais (1494-1553) as '*Les dames montées sur belles hacquenées portaitent chascune ou un épervier, ou un lanneret, ou un émérillon*' (Langford 1912). The Lanner is easy to tame and from the medieval German point of view, this makes it the best choice for hesitant ladies and poets, or the sorts of people whom seem to inexorably lose fine and noble falcons as well beloved partners alike (Whitaker 1905, Dalby 1965, Allen 1980). Yapp (1982) however, points out numerous inconsistencies in various texts that demonstrate that the allocation of various raptor species to medieval social ranks has no basis for support in the real medieval world.

Marco Polo (1298), describing his passage to the city of Ezima, the present Heicheng located in the Ejina district in Inner Mongolia, says about the Lanner: '*Or truova Ezima dopo 12 giornate, che è al capo del diserto del sabion, e è de la provincia di Ta(n)gut. È sono idoli. Egli ànno camegli e bestie assai; e quivi nasce falconi lanieri assai e buoni*'. Throughout his book, Polo mentioned several falcons used for falconry including Sakers, Gyrfalcons and on three occasions Lanners (Bertolucci Pizzorusso 1975). Although he may well have been able to distinguish the three species, it seems quite likely that resident falcons in the vicinity of the Mongolian city were Sakers and that the birds he observed in Qinghai and Xinjiang belonging to Red-naped Shaheen subspecies of the Peregrine (*F. p. babylonicus*).

Pedro Lopez de Ayala (1332-1407), chancellor of the Crown of Castile, undoubtedly recognized differences between the *erlangeri* (*Alfaneque*) and *feldeggii* races (*Borní*; Cummins 1986). In his *Libro de la Caza de las aves et de sus plumages et dolencias et medecinamentos* Lopez says: '*Alfaneque is white with a red nape and they are much requested and after training Lanners were commonly flown in couples, working in harmony and acquiring considerable joint value: 100 francs of gold for a good couple*' (Cummins 1986). Although the name *Lanare* in old English may not correspond to the modern species, laws around the killing or capture of individuals carried fixed penalties in cash and anyone who did not return a lost bird was considered a felon (Yapp 1982). This Act had its origins in the decree promulgated in 1361 by Edward III and written in Norman French regarding '*faucon terselet, lanere ou lanneret, austoure ou autre faucon*' (Yapp 1982).

A presumed Lanner falcon (*faucon dit Lanier*) is mentioned in the archives of the palatial residence of the counts of Artois and Flander at Hesdin (modern Pas-du-Calais department, Northern France) dating from between 1300 to 1315 (Duceppe-Lamarre 2000). Gace de la Buigne, a Norman poet of the late fourteenth century, reported the exceptional longevity of a trained Lanner falcon that reached its twenty-first moult (Lagae 2005). In 1555, Olaus Magnus, a Swedish Catholic ecclesiastic, in his *Historia de Gentibus Septentrionalibus* (History of the Northern Peoples) mentions a *Falco lanarius* in Scandinavia which searched for prey using soaring flight (Magnus 1555).

Several falconry treatises give a description of a falcon species called *blue legs* which can perhaps be attribute to the Lanner falcon (Dalby 1965). Kurt Lindner (1962) states that the *pieds bleus* or *blāfuss* or *blue legs* are always identified as Lanners, both by Albert Magnus and Frederick II of Hohenstaufen, and are separated from young Sakers (Schmidt 1909, Kumerloeve 1963, Dalby 1965). The inference drawn from these references is that the Lanner falcon was common in central Europe during the Middle Ages (Lindner 1962). It seems that the Lanner falcon subsequently became extinct in Germany by the eighteenth century but the term *blaufuss*, due its great semantic value, survived in describing various birds of prey from the Gyrfalcon to Osprey (Schmidt 1909, Lindner 1962, Dalby 1965). Unfortunately, information on the distribution of the Lanner between the fourteenth and sixteenth centuries is scattered and often contradictory although several sources report *the falcon with blue legs* as a breeding species in southern Germany, Switzerland, south east France (Savoie), Czech Republic, Slovakia, Hungary, Poland and Galicia (Lindner, quoted in Kumerloeve 1963). Mayaud (1963) maintains that this is not a sufficiently definitive to identify the species as all *juveniles* of the genus *Falco* show this blue-grey coloration of the ring around the eyes, the cere and sometimes the legs.

In birds, carotenoid pigments are responsible for the yellow colouration of bare skin patches and a reduced access to dietary carotenoids results in a loss of coloration (Brush 1990). The intensity of colour depends on physiological regulation of this pigment as well several other factors such as age, sex, season, health status and body condition, which are revealed when birds have a semi-constant diet such as when they are held in captivity for falconry purposes (Negro *et al.* 1998). The blue and yellow tarsus of Lanner nestlings (*F. b. erlangeri*) in Morocco are greatly influenced by the location of the natal nest (Brosset quoted in Mayaud 1963) a phenomenon also observed in Common Kestrels (Casagrande *et al.* 2009). It therefore seems that this morphological trait that falconry text mention as being derived from practices in handling, feeding and reproducing captive falcons in past centuries may have little diagnostic value for identification to species. So, for example, Pierre Belon du Mans (1555) gave a detailed description of young falcons with blue bare parts which has been identified as true-bred Lanner falcon (Bree 1859). On its wide distribution in France, he wrote: '*il est ordinariement trouvé faisant son aire en notre France'* (Belon du Mans 1555) but it seems more likely that this description refers to the Peregrine falcon. Jaubert and Barthelemy Lapommeraye (1859) and Degland and Gerbe (1867), were careful to avoiding misidentification with other species of falcon, and made an extensive revision of the status of the Lanner falcon in Southern France and concluded by describing it as a vagrant falcon. Accordingly, there is one only confirmed sighting of a *juvenile* near Grenoble (Isère, Rhône-Alpes region) in 1885 (Dubois and Yésou 1986).

Past observations of breeding Lanner falcons (cf. *F. lanarius*) near the village of Wetruschitz (modern Větrušice) in Central Bohemia in the Czech Republic made by Johann Wilhelm von Woborzil (1784-1865) have subsequently been attributed instead to an adult female and five eggs collected from a Saker falcon nest (Woborzil 1846, Mlíkovský 2005a). In addition, there are no evidences of Lanner falcon presence in Medieval Czechia from raptor bones excavated at human sites, artefacts illustrating raptors and/or falconers, of from any literary sources (Mlíkovský 2005b). Adrian Moller, a Dutch falconer, is said to have caught presumed Lanner falcons young in Hungary and trained them for the prince Trautmausdort of Oberweseldorf (Wien, Austria; Woborzil 1846). Again, this is probably a misidentification with the Saker. Nevertheless in the fourteenth century, it is possible that Lanners were traded for falconry as revealed by two leg bones found in the castle area of royal Buda (modern Budapest; Figure 1.2; Gàl 2008). In addition, descriptions of field experiences relating to the capture of wild individuals presents some more plausible details. Charles d'Arcussia (1554-1628), first consul of Aix en Provence, says: '*L'abondance des Laniers Niais viet de Sicile; et font la plus-part leurs aires dans degráds rochers, et par fois aussi au haut de quelque grand arbre. Il en vient aussi de la Poïlle, lesquels se prennent aux montaignes du pays'* (Arcussia 1598). Remarkably, he says that the greater number of these birds come from Sicily, where they build their nests among rocks or the branches of high trees, and also from the rocky areas of Apulia in mainland Italy (Bree1859).

Ulisse Aldrovandi (1522-1605), an Italian naturalist reckoned by Linnaeus and Buffon as the father of natural history studies, in his famous book *Ornithologiae* broadly quoted the treatise of Frederick II as a source for Lanner behaviour (Aldrovandi 1599, Trombetti Budriesi 2000). Aldrovandi (1599) based his classification of the *Lanarius* species on the their geographical origins: *italicus* (from Italy), *gallorum* (from France) and *tunetano* (from Tunisia). Linneaus also maintained this subdivision among presumed Italian (*nostrali*) and French (*forestieri*) birds (Linnaeus 1758, Lorenzi *et al.* 1768). Species accounts in these books seem to present a confusing mix of previous information with less new data, as well as misidentifications among Lanner, Peregrine and Barbary falcons and their *juveniles*. For example, new relationships between European and Maghreb countries added a new *species* termed *tunetano* which is sometimes referred as *Alfanetto* (*Alfaneque* = *F. b. erlangeri*) but classified as *barbaricum* or Barbary falcon (Linnaeus 1758, Lorenzi *et al.* 1768). Nevertheless in the sixteenth-century, ornithology developed into a serious science in Europe and, at the same time, paintings included in manuals were improved greatly by the use of life models whether dead or alive (Olson and Mazzitelli 2007). In fact from a beautiful group of watercolours, a plate made by an Anonymous artist probably represent a *juvenile erlangeri* (watercolor, gouache and black ink with touches of white lead pigment over traces of black chalk - 385 × 284 mm. Inscribed '*le petit sacre*'; Olson and Mazzitelli 2007).

Alonso Martínez de Espinar (ca 1600 - ?), hunter and valet of the real Filippo III and IV, makes reference to the fact that the Alfaneque (cf. *erlangeri* sp.) formerly occupied the Barbary Coast and many individuals were sold in Oran (Algeria; Martinez de Espinar 1644). In his opinion, wild Lanner falcons hunt small prey but well trained birds are capable of capturing partridges, magpies and are also able to pursue, but not necessarily kill, hares (Martinez de Espinar 1644). Not being a species native to Spain, the Lanner falcon, as well as the Gyrfalcon and the Saker, becomes a privileged bird reserved only for rich nobles (Viré 1965). Lanners used for falconry also arrived from Malta as gifts for the royal families of Europe (Hoy 1833, Yarrell 1843). Fenech (2010) listed falcons sent annually by the Grand Master, through its Knights, to the Kings of France, Naples and the King of the two Sicilies. Most of the falcons sent were Peregrines but several *Laniers de Sicile* (cf. *F. b. feldeggii*) and *Laniers de Russie* (cf. Saker; Fenech 2010). In particular from 1706 to 1747, records held in the archives of the National Library of Malta mention three *Laniers de Sicile* and twenty-four birds merely identified as Lanners (Fenech 2010). Bernis (1966) reported a falconry anecdote related in France, that has been associated with various different kings, whereby a male trained Lanner falcon escaped from Fontainebleau and arrived at Malta the next day. The species was also highly prized in Arab countries, in Tunisia in early 20th century for example, and ownership was restricted to upper classes of local governors (cf. Caïd; Whitaker 1905).

Many doubts exist with regard to possible existence of a breeding population of Lanner falcons in Spain both in the past and in more recent times (Bernis 1966). Hartert (1912) suggested the presence of *erlangeri* from North-western Africa rather than *F. b. feldeggii* from Europe. Martinez de Espinar (1644) mentions that the Lanner falcon can be found in the mountainous areas of Leon and other similar provinces. Bernis (1966) gives little credence to past observations in Catalũna, Portugal and Andalucía but confirmed some captures in Almeria and Doñana. Lord Lilford (1833-1896) and Irby (1895) described the use by Lanners of old stick nests of Buzzard *Buteo buteo* on pine-trees in Coto Doñana and Coto del Rey near Sevilla (McGowan and Massa 1990). Of these recorded clutches, one of three eggs is conserved in the collection of the National Museum of Scotland and the Joseph Whitaker collection hold some skins of immature Lanners taken from nests in Coto Doñana, Coto del

Rey and Corio del Rio (Coltart 1952, McGowan and Massa 1990). The evidence therefore seems to suggest that the *F. b. erlangeri* did breed irregularly in limited areas of southern Spain in the 19th century (McGowan and Massa 1990). Other specimens appear to have been collected in Grenada and Murcia but the evidence or these is thin (H. Saunders quoted in McGowan and Massa 1990).

Due to the uncertainty surrounding much of these records, ornithologists have adopted a cautious approach and suggested only that distribution of the Lanner falcon has been limited to isolated populations in the south and south eastern parts of Europe (Hoy 1833, Yarrell 1843, Dresser 1871-1881) or confined to Dalmatia and has only been observed as vagrant in other parts of Europe (Bree 1859, Paris 1921). At the beginning of the twentieth century, the Italian ornithologist Ettore Arrigoni degli Oddi labelled the first *genuine* adult specimen captured in the Abruzzi region as *very rare, cost 60 liras!* (currently 250 Euros; Orlando 1957). In the mid-nineteenth century, Bonaparte (1842) in his *Catalogo* summarized the distribution of the Lanner falcon across Southern and Eastern Europe and into Western Asia. The present distribution of the Lanner falcon in the Mediterranean poses numerous questions (Cramp and Simmons 1980, Glutz *et al.* 1971, Leonardi *et al.* 1992, see also chapter 3). There are several scattered nesting populations among the European Mediterranean countries that should be considered as relicts of a colonization process (see 3.2, Leonardi *et al.* 1992). Historical sources could make a significant contribution to explaining the population dynamics of the Lanner falcon in the recent past but unfortunately these do not always have a scientific basis and may be unreliable (Lindner 1962, Kumerloeve 1963, Mayaud 1963). The analysis of ancient texts reveals many morphological, behavioural and ecological inconsistencies which can generate a great deal of confusion (Dalby 1965, Evans 1967, Battaglia 1977) and many ancient Authors are often unaware, for example, that the plumage of many young raptors differs from that of the adult, or of the differences between males and females of the same species (Mayaud 1963, Arnott 2007).

1.3 Names

Like many other uncommon bird species, the Lanner falcon did not have a proper noun in ancient times. Aristotle and ancient Greek sources refer to all diurnal raptors smaller than Eagles as *Hierax* (ἱερος = sacred; Arnott 2007). They were sacred both to Apollo and Hermes (Ael. Nat. An. XII, 4) and fed on select food as offering to the gods. This name certainly includes the Peregrine (*Kirkos*) and probably other Peregrine-like species such as the Lanner and the Saker that hunt pigeons with fast stoops and nest on steep rock cliffs (Arnott 2007). Other generic names for such groups are *Thēreutēs* (Hunter) and *Panthēr* which may refer to the spotted plumage of young birds (Arnott 2007). Given that such names cover a range of species, it is difficult to reconstruct the history and evolution of the common name for the Lanner falcon (Evans 1967). As consequence it is difficult to discern when the common name *Lanner* is used as a synonym of the specific name *F. biarmicus* (Evans 1967).

Falco comes from the late Latin *falx* (derived from late Greek *phalkōn*) meaning *sickle*, a reference to the shape of the wings during flight (Clark 1999, Jobling 2010). According to Servius Honoratus (390-480 AD) another possible explanation could be a reference to the shape of the talons '*quod ungues more fàlcis habeat introrsum flexos*' (Salvadori 1887). In the opinion of C. J. Temminck, the name *biarmicus* was composed of the root *bis* (two) and *armicus*, therefore with two beard stripes (Temminck 1820-1839, Jobling 2010). Almost certainly, Coenraad Temminck used the original Linnaean description *biarmicus* as synonymous with *bearded* in reference to its moustached appearance (*Faucon biarmique*; Temminck 1820-1839, Jobling 2010). Following this, several subsequent Authors used the common name *Double-bearded falcon* which has not been adopted over time (Cuvier *et al.* 1827, Cavendish Taylor 1859). Actually, Linnaeus also used the term *biarmicus* to describe another bird, the small Bearded Reedling *Panurus biarmicus* with males that show black moustaches (Linnaeus 1758). He described this passerine bird as inhabiting Biarmia (Bjarmaland, the ancient name of northern countries) or possibly suggested a locale by using Latinised the name *Parus beardmanicus* (Beardmanica or Beard Manica of Jutland) from Albin (1738). Temminck and Cuvier interpreted as *bis-* the syllable *bi-*, rather than regarding the epithet as a geographic toponym (Jobling 2010). Thus, the attempt by Steyn (1983) to translate this name as doubly-armed in reference to the added tooth which is found below the tip of the point of the beak is somewhat improbable. In terms of the names applied to subspecies of the Lanner falcon, *tanypterus* comes from Greek *tanupteros* meaning with extended wings, *abyssinicus* from Abyssinia (modern Ethiopia), *erlangeri* from Carlo von Erlanger (1872-1904) a German naturalist, and *feldeggii* from Col. Christoph von Feldegg (1780-1845) Austrian army officer and naturalist (Jobling 2010).

Many problems therefore arise when attempting discern the origin of the name Lanner/*Lanier* (Evans 1967). As mentioned above, neither the Greeks nor the Ro-

Table 1.6 Common names of the Lanner falcon in various languages including local dialects (Abuladze 2013, Abuladze *et. al.* 1991, Andrews 1995, Baranauskas V. pers. comm., Bernis 1966, Bernis *et al.* 1994, Bonan A. pers. comm., Clark W. S. pers. comm., Corriente 2008, Cramp and Simmons 1980, Dean 2000, Dehelean A. pers. comm., Demir O. pers. comm., Elmoghrabi L. pers. comm., Essetti I. pers. comm., Fenech 2010, Fenech pers. com., Getraide and Hatzofe 1991, Goodman and Meininger 1989, Herz 2004, Khoury F. pers. comm., Issi E. pers. comm., Louwrens 2004, MacLean 1984, Massa 1985, Mayol *et al.* 2006, Morsy H. pers. comm., Naudžius A. pers. comm., Peltomäki J. pers. comm., Prakljačić D. pers. comm., Sandberg 1992, Sherman D. pers. comm., Stratford J. pers. comm.,Vlachos C. pers. comm., Yosef 1988).

Afrikaans	Edelvalk (Noble falcon)
Albanian	Skifteri i Mesdheut (Mediterranean falcon)
Arabic	Saqr sabasibi (صقر سباسبي), Lanner (الوكري), Hur Arabi (Jordan)
Armenian	Միջերկրածովային բազե (Mijyerkratzovyan baze - Mediterranean falcon)
Azerbaijani	Aralıq dənizi qızılquşu
Bulgarian	Далматински сокол (Dalmatian falcon)
Catalan (incl. Balears)	Alfanec, Falcó Llaner
Croatian	Krški Sokol (Rock falcon)
Czech	Raroh jižní (Southern Saker)
Danish	Lannerfalk
Dutch	Lannervalk
English	Lanner Falcon, Lanner
Estonian	Könnupistrik
Finnish	Keltapäähaukka (Yellow head falcon)
French	Faucon Lanier, Lanier
German	Lannerfalke, Feldeggsfalke, Lanner
Georgian	წითურთავა ბარი (წითურთავა გავაზი, წითელთავა შავარდენი), (Tsithurthava bari, syn. Tsithurthava gavazi, Tsithelthava shavardeni)
Greek	Χρυσογέρακο, Chrisogerakas (Golden Falcon)
Hungarian	Feldegg-sólyom (Feldegg's falcon)
Icelandic	Slagfálki
Iranian (Persian)	Lachan-e ma'muli
Israeli	בז צוקים Baz Tzuquim (Tsukim) (Cliffs falcon)¬
Italian	Falcone Lanario, Falco Lanario, Lanario
Japanese	ラナーハヤブサ Ranahayabusa
Kurdish	Baz
Latvian	Rudgalvas piekūns
Lithuanian	Viduržeminis sakalas (Mediterranean falcon)
Macedonian	Далматински (Јужен) сокол (Dalmatian/South falcon)
Maltese	Borin, Bies Rar (Rare falcon), Bies Rasu Qastnija (Chestnut-headed Falcon)
Montenegrin	Krški soko (Rock falcon)
Norwegian	Slagfalk
Polish	Raróg górski (Cliffs falcon)
Romanian	Soim sudic (Southern falcon)
Portuguese	Borni, Alfaneque
Portuguese (Angola)	Falcão-de-nuca-vermelha
Russian	Средиземноморский сокол (Sredzemonmorsky Sokol/Mediterranean falcon), пушистый сокол (Pušistyï sokol) Ланнер (Lanner)
Serbian	Krški sok, Кршки соко (Rock falcon)
Sicilian dialect	Pinniciaru (Partridge killer)
Slovak	Sokol tmavý
Slovenian	Južni sokol
South Africa dialects	Kakodi (K), Pekwa, Sepêkwa (NS), Phakoé (SS), Rukdozi (Sh), Rikhozi, Rigamami (Ts), Phakwê (Tw), Uketsche (X), uHeshe (Z).
Spanish	Halcón Borní
Swedish	Slagfalk
Turkish	Biyikli Doğan (Falcon with moustache stripes)

mans gave a specific name to the Lanner falcon and Frederick II also recognized it as one of a large group of '*desert falcons*' (Wood and Fyfe 1943). Nevertheless, Theodore of Antioch in his Latin version of *Moanim* seems to adapt the Arabic names *anūqi* and *anīqī* as *aynoki* and *aynoli* later translated into French as *aynolu* (Marruncheddu 2008). Another explanation was given by Yapp (1982) who suggest that the first occurrence of *Laner* in the twelfth century (*Lanret* in the 15th century) was due to the translation from late Latin *tardearius* mentioned in the book *Suppletio defectum* (1216) written by the English scholar and teacher Alexander (of) Neckam (1157-1207). In turn, *tardearius* comes from *tarda* (cf. Great bustard) one of the presumed preferred prey of the Lanner falcon (Yapp 1982).

Unfortunately, the Latinisation of the common name for taxonomic purposes (*Falco lanarius*) produced further confusion. This name does not seem to have come, as some authors have suggested, from comparing the softness of the plumage to that of wool: '*Lanarius, vel a laniandis avibus, vel quod plumas multas, densasque et molles im modum lanae habeat*' (Aldrovandi 1599, Evans 1967). Another presumed origin is from *laniare* (butcher) in reference to the process of prey consumption (Buffon 1770). The Middle English name *Laner*, derived from the Middle French *Lanier*, was first used between 1250 and 1300. Since the twelfth and thirteenth centuries, the falcon species generally designated as *Lanet*, *Lanette* or *Lanier* also included at least forty names used in several falconry treatises (Lindfors-Nordin and Gamillscheg 1937). In his monograph, Evans (1967) suggests that *Lanier* evolved independently rejecting the hypothesis that *lanarius* equates to *lanier*. In the falconry terminology adopted in the Middle Ages, adjectives such as *gruier* and *haironier*, described raptors trained to pursue cranes and herons respectively (Lindfors-Nordin and Gamillscheg 1937). A related term is *anier* used to describe bird of prey trained to attack ducks (singular *ane*, *anet*, *anette* plural *anes*, *anets*; Lindfors-Nordin and Gamillscheg 1937, Evans 1967, Abeele 1990). In the *Totius Latinitatis lexicon*, Egidio Forcellini (1688-1768) named this falcon *anatarius* (presumably from the fourth century; Evans 1967). Through the agglutination of the French definite article *le*, *l'anier* became more easily associated with the precise name of a falcon species than *gruier*, giving the term *Faucon lanier* (Lindfors-Nordin and Gamillscheg 1937, Evans 1967, Abeele 1990). In addition, a tricky homonymy was avoided because *anier** in the thirteenth century also meant donkey herder (Lindfors-Nordin and Gamillscheg 1937). Thus, a particular word from the French falconry dictionary easily become cosmopolitan by an adjustment process into the Latin, Catalan, German and English languages (Lindfors-Nordin and Gamillscheg 1937). In France during the sixteenth and seventeenth centuries, poets compared the hesitant behaviour of lovers to the Lanner that generally avoids attempting to capture very large prey such as cranes and herons (Evans 1967, Abeele 1990). In the *Booke of Hawkyng after Prince Edwarde Kyng of Englande* later adapted in the compilation *Boke of Seynt Albans* (1486), *Lanare* and *Lanrett* already being used for female and male Lanner falcons respectively (Cummins 1988, Pickering and O'-Mara 1999). Later, the old spelling *Lanrett* turned into the final form *Lanneret* (Walker 1999).

Other names associated with the Lanner include *Dogàn* (Turkish) and *Seifee* (Cilicia, Turkey), *Laneret*, *Laner*, *Lenier*, *Lanierer Passager* in French, *Terzolo Laniero* (*Laniero*) in Italian, *Lanoy* in Savoia, *Lanete*, *Lanet*, *Lanette*, *Lanetefalck*, *Lanetenfalck*, *Lanierfalck* (German), *Lannar* (English) and *Lanero* (Spanish, starting from 1368) (Aldrovandi 1599, Brisson 1760, Sestini 1785, Harting 1841, Schmidt 1909, Evans 1967). *Sweimer*, *Swemmer*, *Schwemmer*, *Schweymer*, *Schwimmer*, *Schweimer* (*Lanete*), *Swemere*, *Schmeymer*, *Schwimmer* and other variations were also used before the seventeenth century in Germany for both Lanner falcons and Buzzards (Schmidt 1909). Aldrovandi (1599) explains that this name probably comes from the gliding flight of *Lanarius* that makes it appear to '*swim*' in the air. Further names from German falconry related to duck hunting include *anat-habech*, *anet-habech* and *anot-hapuh* (Lindfors-Nordin and Gamillscheg 1937, Evans 1967). The medieval Italian name *Falcone Laniero* was derived from Brunetto Latini's French falconry treatise translated by Bono Giambono in 1474 (Lindfors-Nordin and Gamillscheg 1937).

Some modern European languages incorporate the name *Lanier* (e. g. English, German, Italian, Danish and Dutch) but other names have completely different roots (Table 1.6). In Russian, the name *Sredizemnomorsky Sokol* (Mediterranean falcon) was used to differentiate the Lanner from the Saker falcon (Dementiev and Gladkov 1951). This name is no longer in use and Lanner has been transliterated into Cyrillic script (*Ланнер*; Abuladze *et al.* 1991). The term Mediterranean falcon is still used in Albania, Armenia and Lithuania (Table 1.6). Other common names refer to geographical areas (Bulgarian, Czech, Macedonian, Romanian), plumage and morphology (Finnish, Greek, Maltese, Portuguese speech in Angola, Turkish) or preferred breeding sites (Croatian, Israeli, Montenegrin, Polish, Serbian; Table 1.6). In German and Hungarian the *F. b. feldeggii* race was named in honour of the General Baron von Feldegg when the first specimen was caught in Dalmatia in 1829 (Table 1.6; Salvadori 1887).

In the nineteenth century, the nominal race *biarmicus* of South Africa occasionally was called *Lakatoo falcon* (Gurney 1860, 1862). In addition, there are numerous names in local dialects which are limited to small regions of the species range (Table 1.6). In the Sicilian dialect the Lanner is referred to as *Pinniciaru*, which means '*partridge killer*' (Massa 1985). Other Sicilian names (such as *Falcuni raro* meaning Rare falcon, and *Cappuccina*) were mentioned by Giglioli (1889). In one of the South African dialects (Humbe) the Lanner is called *Lucoi* and *Kuata-andimba* '*hare killer*', with has no basis in fact, and in the Basuto oral tradition as *Phakui* (cop; cf. *Phakweyabadisa;* Layard and Sharpe 1875, Langford 1912). In the Zulu-speaking areas, *uheshe* (used for both the Peregrine and the Lanner falcons) derived from the ideophone *heshe* which means '*of swooping onto*' or '*of snatching in flight*' (Koopman 2002). Birds like falcons are often grouped together and treated as a morphotype with a unique indigenous name so called ethnospecies which possibly transcend genus and species (V. Williams pers. comm.). Zulu and Xhosa are very similar languages and, although names are slightly different (*uheshe*, Zulu, and *ugeja* Xhosa), they have a similar sound when spoken (Godfrey 1941, V. Williams pers. comm.). According to Anderson (1872), *Onikothé* is the name used in the Damaraland (nowadays in the Kunene region of Namibia). Latham (1821) and Salvadori (1884) reported that in Abyssinia (the modern Ethiopia) the Lanner falcon is referred to by natives as *Goodie goodie* and locally as *Scita* (Shewa, an historical region of Ethiopia) and *Aderghemit* (Oromo language). Cornwallis Harris (1844) identified the Honey Buzzard *Pernis apivorous* as *Goodie* and the Lanner as *Ya Amora Alaka* (the king of birds of prey) capable of stealing prey from the Lesser Spotted Eagle *A. pomarina*. In several districts of Angola, Bocage (1880) mentioned *Lucoi* (as in Humbe) and *Lupamba* (Caconda, Huíla Province). In the Hausa language, spoken in the former territory of northern Gobir (Central Niger), its name is *shaho madauki* where *shaho* is the generic name for a bird of prey and *madauki* refers to a raptor that picks things off/up (Manvell 2010). In Tamahaq, the Northern Tuareg language spoken in Algeria, western Libya and Northern Niger, the Lanner falcon is called *Aloullem* (as well the Common Kestrel) and *Afokka* (Wacher *et al.* 2005). People in the Gabù region of Guinea-Bissau call it *Segheleere* (in Peulh language) which is actually used for many medium size birds of prey (G. Carron pers. comm.) as well *Quieli* in Senegambia.

Arab names of falcons were formed *ex novo* rather than from a Romanized derivation of *falco-nis* (Martinez Enamorado 2011). On a lexical level, Arabisms in Castilian are particularly numerous in names of wildlife and plants (Neyrod 2004). Pedro de Alcalá (1505), a Spanish priest, in his dictionary of the Arabic dialect spoken in Granada stated that the general term used for falcon/goshawk in al-Andalus was *bāz* (pl. *bīzān*). The term *bāz* is Persian (Goshawk *sensu strictu*) and means falcon in both modern Hebrew and Arabic (*bāz*, Table 1.6). Since the fourteenth century in Spain, the Lanner has been called Halcón Borní (*burnī* – Maghreb countries) derived from the Arabic *burniyy-īn* to separate it from the North-West African subspecies called *Alfaneque* (*fanāka-fanāk*, *Alfphanet* by the falconers in the Christian Middle Ages; Alcalá, de 1505, Baist 1880, Martinez Enamorado 2011). In medieval Tunisia it was also referred to as *burnī šaršūm* (errant) and *šwīraf* (noble; Viré 1977). *Alfaneque* (synonyms: *Alfegue*, *Alfeque*, *Alfrag*, *Alphamet*) is currently in use in the Portuguese language and the variant *Alfanec* was also used in Catalan (Herz 2004, Corriente 2008). This name comes from Western Arabic *bāz alfanak* literally '*falcon for hunting fennecs*' (Corriente 2008). This name has no basis in either the prey taken by wild populations nor in falconry practice. Perhaps it is a corruption of Andalusi Romance **al+xal+AYQ* which means '*from the wilderness*' which is rather suited to a species belonging to inner desert areas far from the coast (Corriente 2008). The ancient name *Saqāwā/Saqāwa* (pl. *Saqāwiyyāt*) meant Lanner falcon in ancient Syria and Egypt but now is used by falconers for a '*variety*' of female Saker (Allen 1980, Viré 1966, 1977, 1984). Old falconers of East Islām called the less familiar male Lanner falcon *šāhīn kūhī l-bahr* (Peregrine of mountains and coasts) and *dakar al-sunqūr* (Gyrfalcon tiercel; Viré 1977). The *Falconidae* group was called *faṣīlat al-ṣaqriyyāt* and the *Falco* genus *ğins al-ṣuqūr* (Viré 1966). Ibn Hishām al-Lakhmī writing in the twelfth century stated that the term *ṣaqr* was used to refer to any birds of prey employed in falconry including falcons (*al-buzat*; Martinez Enamorado 2011). Currently, *saqr* or *sakr* (رقص, the *q* and *r* are mixed together) indicate all species included in the genus *Falco* (I. Essetti pers. comm.). The *Novitates Zoologicae* reported a certain respect towards this species by the Arabs (cf. *erlangeri* sp.) to which they give the name *Tair* or *Tair-el-Or* or '*noble falcon*', the same term used in Afrikaans (Table 1.6; Whitaker 1905, Hartert 1915). Nevertheless, for the Muslim West all *Falconidae*, including the Lanner falcon, are considered noble (*hurr*; Gurney 1871, Whitaker 1905, Viré 1961, Martinez Enamorado 2011). In particular, *tayr hurr* (noble bird) is used for the Lanner but also for the Barbary falcon, the Eleonora's falcon and the Sparrowhawk *Accipiter nisus* (Viré 1961). Gurney (1871) listed several species of falcons used for falconry by Bedouins in Algeria and identified the Lanner as *El Meguerness* and considered *El Bourni* as the Barbary falcon.

However, the Arabic names of birds remain confusing, because each Arab country uses its own local names, or in some cases the same name can be used to refer to a number of different species (I. Essetti and F. Khoury pers. comm.). An example of a provincial name is that used in Benghazi (Libya) where the Lanner falcon is called *Gernaz* (Hamza *et al.* 2008). Further problems arise with regard to confusion with the Saker falcon. For instance, Jordanian Bedouin falconers prefer Sakers to Lanners and this may well be why there are various names for Sakers which vary slightly in size and colouration, some being palerthan others (F. Khoury pers. comm.). Therefore, names for the Lanner are frequently the same as those used for the Saker and its variants (*Saqr Hurr*, *Saqr Hor*, *Saqr Al-ghazaal*, *Saqr wakri*) or the Peregrine (*Saqr shaaniin*, *Shahin wokri*; Heuglin and Finsch 1869, Upton 2002, L. Elmoghrabi and F. Khoury pers. comm.). A possible solution would be to adopt a new modern name for the species. In fact, the Tunisian committee on Arabic bird names proposed *Sakr sabasibi* (يبسابس رقص; falcon of plains and steppes) in keeping with the ecology and behaviour of the Lanner (I. Essetti pers. comm.). For the time being however, the precise transliteration of the name Lanner falcon into Arabic is still used (يركولا).

1.4 Taxonomy

There is no falcon about which so much confusion has existed as the celebrated Lanner of falconry.

Subclass	*Avialae* Gauthier 1986
Infraclass	*Aves* Linnaeus 1758
Parvclass	*Neornithes* Gadow 1893
Cohort	*Neognathae* Pycraft 1900
Subcohort	*Neoaves* Sibley *et al.* 1988
Division	*Terrestrornithes* new taxon
Subdivision	*Dendrornithes* Verheyen 1961
Section	*Raptores* Baird 1858
Superorder	*Falconimorphae* Seebohm 1890
Order	*Falconiformes* Seebohm 1890
Suborder	*Accipitres* Vieillot 1816
Infraorder	*Falconides* Sharpe 1874
Family	*Falconidae* Leach 1820
Subfamily	*Falconinae* Vigors 1824
Genus	*Falco* Linneaus 1758
Subgenus	*Hierofalco* Cuvier 1817
Species	*Falco biarmicus* Temminck 1825
Subspecies	*F.b. biarmicus* Temminck 1825
	F.b. abyssinicus Neumann 1904
	F.b. tanypterus Schlegel 1844
	F.b. erlangeri Kleinschmidt 1901
	F.b. feldeggii Schlegel 1843

Table 1.7 Classification of the Lanner falcon according to Livezey and Zusi (2007), based on comparative anatomy.

The name has been given to the Peregrine, the Ger-Falcon, the Sacer, and other birds, even by scientific writers. We are indebted to H. Schlegel for applying the right name to the right bird, and for making the distinction between this and preceding species, which will prevent any future confusion (Bree 1859). Charles R. Bree summarizes the great confusion arising from past errors in the identification of the Lanner falcon and concluds by thanking Hermann Schlegel for the new taxonomic revision, a re-classification that continues to persist persist almost unchanged until the present day (Table 1.7).

Prior to this, few naturalists were able to correctly identify the Lanner falcon and no public or private collections held any specimens (Yarrell 1843, Bree 1859, Hartert 1915). Schlegel (1843) argued that Buffon (1770) and Pennant (1768) misidentified a young female Peregrine as a Lanner falcon (Yarrell 1843). Emma Phipson (1883) reported that it was because of this that Lanner falcon was believed to be resident in Britain. Such misidentifications are also evident in the more distant past. For instance, a bird inventory made in 1274 locate a *ayeria falconum lanerium* in Lundy (Bristol Channel) a well known Peregrine site (Yapp 1982). Likewise, Brünnich and Mohr described the Merlin under the name of Lanner falcon (Schlegel 1844).

In addition, the description of the *Falco lanarius* in the *Systema Naturae* by Linnaeus (1758) more closely matches a Gyrfalcon, a description which was probably derived from a young bird killed in Sweden. Montagu (1802) agreed with Linneaus who considered that the Lanner falcon was a species inhabiting northern Europe (Iceland, Faroe Islands, Denmark and Sweden). Later, Nilsson (1858) in the last edition of his book *Birds of Scandinavia* renamed the species in Swedish *Slagfalk* as distinct from the Gyrfalcon. In 1761, Linnaeus also wrote that this bird was *distinctissimus a Lanario*

Falco lanarius = *feldeggii and tanypterus* ssp.
Falco lanarius græcus = *feldeggii* sp.
Falco lanarius nubicus = *tanypterus* sp.
Falco lanarius cervicalis = *biarmicus* sp.
Falco lanarius capensis = *biarmicus* sp.
Falco lanarius alphanet = *tanypterus* sp.
Falco laniarius (*see Falco lanarius*)
Falco rubeus (see page 15)
Falco tanypterus = *tanypterus* sp.
Gennaia lanarius = (*see Falco lanarius*)
Gennaia laniarius = (*see Falco lanarius*)
Gennaia Feldeggi = *feldeggii* sp.
Gennaia tanypterus = *tanypterus* sp.
Gennaia biarmica = *biarmicus* sp.
Falco Feldeggii = *feldeggii* sp.
Falco cervicalis = *biarmicus* sp.
Falco b. graecus = *feldeggii* sp.
Falco b. feldeggi = *feldeggii* sp.
Falco chicqueroides = *biarmicus* sp.
Falco capensis = *biarmicus* sp.
Falco H. erlangeri = *erlangeri* sp.
Falco H. tschusii = *erlangeri* sp.
Falco aroeris (see page 10)
Hierofalco feldeggi = *feldeggii* sp.
Hierofalco erlangeri = *erlangeri* sp.
Hierofalco biarmicus = *biarmicus* sp.
Hierofalco tanypterus = *tanypterus* sp.
Falco biarmicus orlandoi = *feldeggii* sp.

TABLE 1.8 Synonymous and presumed subspecies of the Lanner falcon from the mid-nineteenth century to the early twentieth century.

Italico (Fauna Suec ed 2, p. 22), agreeing with the previous classification proposed by Aldrovandi (1599). Hartert (1912) correctly noted that the *Lanarius* of Linnaeus does not correspond with the *F. lanarius* (= *F. tanypterus*) of modern taxonomy.

Dresser (1871-1881) excluded the Lanner as a breeding species from North Germany, Netherlands and France and reported an erroneous identification of a young peregrine captured in Germany by H. Schlegel. Based on the occurrence of museum specimens, the Lanner become a very rare species in Malta, Greece and also in Italy due to the very rare capture of adults. Most specimens found in museums seem to be mainly wandering immature birds (Dresser 1871-1881, Martorelli 1911).

As a result of this considerable taxonomic confusion, also the inexistence of the Lanner as a species separate from the Peregrine has been proposed (Malherbe 1843). In fact, Benoit (1840) and previously Savi (1827) considered the *Faucon Lanier* as one of the numerous synonyms of the Peregrine falcon. A. Malherbe, who observed many specimens from several collections, says: '*J'ai vu des faucons pelerins ou gerfauts jeunes etiquetes sous le nom de Lanier, mais ces erreurs ne doivent pas faire obstacle a l'existence reelle des deux especes; elles prouvent seulement que le lanier est rare et peu connu*' (Malherbe 1843). In his opinion, the Lanner is merely a rare and little known falcon with two recognized forms: the *veritable* European *Falco lanarius* and the *prétendu* African *Falco tanypterus* (Malherbe 1843).

On the other hand, Baird *et al.* (1875) increased the number of subspecies and classified as American Lanner falcon *Falco lanarius* var. *mexicanus*, the Prairie falcon *F. mexicanus* using ecological, morphological and functional similarities between these species. More recently, Ripley (1982) and Sibley and Monroe (1990) reduced the Laggar falcon of the Indian sub-continent as from a distinct species to subspecies of the Lanner *F. b. jugger*.

Schlegel (1843) himself described as a new species a falcon under the name of *Falco Feldeggii* but soon reverted its name as *Falco lanarius* certain to be the *true* Lanner of Belon du Mans (1555), and the Lanner of old falconers (Schlegel 1844, Schlegel and Verster van Wulverhorst 1845-1853, Sharpe 1874, Langford 1912). The specimen, collected from Dalmatia, was considered by Johann Natter (1787-1843) to be a Barbary falcon which was then classified as a new species by Schlegel (Schlegel 1844). Another proposition was made by Gurney that identified the *nubicus* as the real *lanarius* (Bree 1895).

Confronted with a large number of taxa, Strickland (1840) felt justified in uniting a number of species including *F. chiqueroides*, *F. rubeus*, *F. lanarius*, *F. cervicalis*, and *F. feldeggii* under a single species name of *Falco biarmicus* (Table 1.8). He saw this species as essentially African extending from the Cape region to Egypt with a satellite populations in Greece and the Balkans, with occasional wandering individuals found in central Europe (Strickland 1840). Dresser (1871-1881) suspected that in the past the species name *F. lanarius* had been used primarily to identify the Saker.

In spite of these debates, most of these names were assigned on the basis of morphological traits which in turn are considered distinctive for the Lanner falcon complex. For example the rufous cervix of the Lanner suggested the name *F. cervicalis* and indirectly *F. chiqueroides* due the similarity with the Red-necked Falcon *Falco chicquera* (Cavendish Taylor 1859).

In the nineteenth century, the Lanner falcon was in fact often considered a very rare and possibly vagrant species with, for example, only one capture reported and a solitary confirmed nest site in South-east Sicily (Savi 1827, Salvadori 1887, Giglioli 1889).

For Arrigoni degli Oddi (1929), the Lanner was a resident species found breeding in Italy and Latium but only infrequently in other Italian regions. Martorelli (1911) also adopted the sub-genus *Gennaja* in order to distinguish '*northern falcons*', or Lanner falcons, from Peregrine the Saker falcons as union between *F. b. feldeggii* and Gyrfalcons. He also did not accept the trinomial nomenclature and the classification proposed by Whitaker (1905) that considered the *F. b. feldeggii* race inhabiting Tunisia.

As a consequence of scarcity, many of these controversial taxonomic issues came from about due to the low number of occurrences of the Lanner falcons, especially in Italy and Balkans, and there seems to have been less controversy in North and South Africa where the species is more abundant.

In fact, the most ancient scientific note entirely devoted to Lanner falcon biology was published regarding a breeding site in Egypt (Cochrane 1864). Cochrane visited a nest in the south side of the Third Pyramid of Giza around nine metres from the top and found four eggs (two addled, two incubated) which he depicted in a colour plate at the end of the short note (Cochrane 1864).

1.5 Systematic and genetics

The phylogeny of the Falconidae *group*

Recently, Livezey and Zusi (2007) made an extensive analyses of the phylogeny of birds based on comparative anatomy (Table 1.7). Nevertheless, the rapid radiation and diversification of modern birds (*Neoaves*) poses numerous problems with regard to the evolutionary relationships among *taxa* (McCormack *et al.* 2013). In fact, the numerous methodological approaches (morphology, DNA-DNA hybridization, whole mitochondrial genomes, different nuclear exon, ribosomal RNA and intron sequences) often give conflicting results (see Livezey and Zusi 2007 and Hackett *et al.* 2008 for reviews). Generally, both molecular and morphological phylogenetic studies support an early split among *Paleognathae* (ratites and tinamous) and *Neognathae* (all other birds) and a second, later split that formed *Galloanserae* (chickens, ducks) and *Neoaves* (the majority of birds) from neognaths (Hackett *et al.* 2008, McCormack *et al.* 2013). McCormack *et al.* (2013) using sequence data from ultra-conserved elements (UCEs) of loci for 32 members of *Neoaves*, defined monophyletic waterbird (*Aequornithes*) and landbird clades that diverge deep in the *Neoaves* phylogeny (Figure

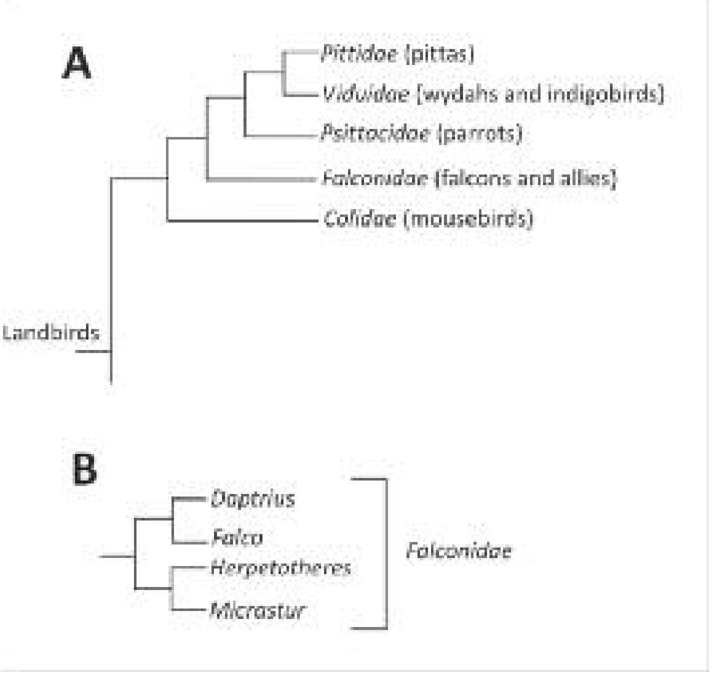


FIGURE 1.5 Relationships between passerines and parrots with falcons as sister group (A) and among genera of *Falconidae* (Hackett *et al.* 2008, Suh *et al.* 2011, McCormack *et al.* 2013, Yuri *et al.* 2013, Li *et al.* 2014).

1.7A). Previously, Hackett *et al.* (2008) found a unexpected close relationship between passerines and parrots with the *Falconidae* as a sister to this clade (Figure 1.5 A, B).

Afterwards, Suh *et al.* (2011) supported the sister group relationship between passerines and parrots (*Psittacopasserae*) and their mutual affinity to falcons (*Eufalconimorphae*) using rare genomic changes encoded in retroposons (Figure 1.5 A). In addition, phylogenetic trees from 1541 locus analysis provided strong support for the absence of a sister relationship between raptorial birds in the *Accipitridae* and *Falconidae* families (McCormack *et al.* 2012). Thus, *Falconidae* are not members of the *Accipitriformes* and in contrast to ancient authors, Linneaus and traditional systematic definition (grouping organisms by their similarities in appearance and structure) as well as DNA-DNA hybridization, falcons become more closely related to parrots rather than hawks (Figure 1.5 A; Sibley and Ahlquist 1990, Livezey and Zusi 2007). As consequence, the AOU check-list of the Birds of North America and the IOC World Bird List included raptor families *Cathartidae*, *Accipitridae*, *Sagittariidae*, and *Pandiondae* in the Order *Accipitriformes* with the *Falconidae* separated as the Order *Falconiformes* (Chesser *et al.* 2012, Gill and Donsker 2013). Nevertheless, new discoveries may mean that further analysis becomes necessary especially in relation to the effects of gap accumulation (Yuri *et al.* 2013).

Lanner falcon subspecies

The history of the taxonomy and systematics of Lanner falcon subspecies in the modern era is deeply connected with the Rijksmuseum van Natuurlijke Historie of Leiden (RMNH) and its first two directors: Coenraad Jacob Temminck (1778-1858) and Hermann Schlegel (1804-1884) (Hoek Ostende *et al.* 1997, Gassó Miracle 2008). Given the fluid nature of zoological nomenclature ar the beginning of the nineteenth century, the main merit of the approach used by Temminck was to avoid the exponential growth in the number of taxa by splitting genera on the basis of morphological traits (Gassó Miracle 2008). He was mainly concerned with describing the fauna of Dutch colonies such as Cape Province, from where he received a specimen for his *Falco biarmicus* (Temminck 1820-1839). This species account, as along with many other new ones, was published in his continuation of *Buffon's Planches coloriées* in 1825 (Temminck 1820-1839, Hoek Ostende *et al.* 1997). H. Schlegel defined the *Falco Feldeggii* of Europe and *Falco tanypterus* of Egypt and '*Nubia*' in several publications, sometimes in mutually contradictory accounts (Schlegel 1843, 1862). R. B. Sharpe treated these distinct species and confined the former to countries bordering the Mediterranean and only rarely found in Central Europe and in Egypt and North-east Africa, whereas he considered *F. tanypterus* a closely allied inter-tropical representative in North-east and West Africa (Gurney 1880). Gurney (1880) also thought that these two races were one species because their distribution overlaps

Plate I

5 cm

Falco biarmicus feldeggii

Falco biarmicus erlangeri/tanypterus

Falco biarmicus abyssinicus

Falco biarmicus biarmicus

Group	Plumage patterns	Wing (mm) (female)	Distribution
I Underparts brownish pink or reddish isabelline			
F. b. biarmicus	Less spotted underparts or little spots on the flanks	up to 370	Southern and Eastern Africa
F. b. abyssinicus	Largerly spotted underparts	up to 385	Tropical East and West Africa
II Underparts pale or only slight washed-out reddish			
F. b. erlangeri	Little spots on the flanks, crown and nape pale reddish or yellow	up to 355	NW Africa (Tunisia, Algeria)
F. b. tanypterus	Bright colours than *erlangeri* but less than *abyssinicus*, slightly larger than *erlangeri*.	up to 375	NE Africa (Egypt and N Sudan)

Table 1.9 Main diagnostic features (plumage patterns and wing measurements) used for describe Lanner falcon subspecies (Temminck 1820-1839, Schlegel 1843, 1862, Kleinschmidt 1901, Neumann 1904, Hartert 1902, 1912, 1915).

and they are hence inseparable as subspecies.

A group of German naturalists and ornithologists provided the first detailed descriptions of the subspecies of the Maghreb and the Horn of Africa (cf. *F. b. erlangeri* and *F. b. abyssinicus*). They travelled mainly in Tunisia, Morocco, Algeria, and Ethiopia collecting, measuring and analysing colour patterns and morphological traits of numerous specimens and eggs (Erlanger 1898, Kleinschmidt 1901, Neumann 1904). C. von Erlanger (1898) reported that the Lanner was the most common falcon that he had seen during his journey, especially as breeder species of the Southern mountainous areas. This new quantitative data, together with those from other subspecies, allowed the development of the *Formkresis* theory proposed by O. Kleinschimidt (1901)(see Chapter 10).

In volume XXII (1915) of the journal *Novitates Zoologicae* there is a full section on '*Lanner Falcons*' containing detailed anatomical descriptions of all subspecies and the modern systematic collocation of these birds (Hartert 1915). Successive handbooks (Glutz *et al.* 1971, Cramp and Simmons 1980, Brown *et al.* 1982, Del Hoyo *et al.* 1994) re-confirmed these descriptions which had already made in 1915. Nevertheless, some researchers consider North African subspecies as identical (Clark 1999) or classify *F. b. tanypterus* as an intermediate form between *F. b. erlangeri* and *F. b. feldeggii* (Forsman 1999). This lack of unique features among races had also been noted by Hartert (1915) when he wrote '*One can easily understand that* erlangeri *was not separated* *from* tanypterus*, as they are hardly separable, though the former is certainly a little smaller. Single copies of* F. b. tanypterus *are not always sure of those of* F. b. erlangeri *to distinguish'* (Hartert 1912). Neumann (1904) came to the same conclusion based on a comparison between the wing measurements of the two subspecies and those of the *abyssinicus*. By way of support for this new race, he examined specimens from Abyssinia (= Ethiopia), Northern Abyssinia (= Eritrea) and Southern Egypt. At the same time, he recognized a large variability among individuals from northern and southern Abyssinia, as well as the sole specimen he had available from Togo, which he considered pale (Neumann 1904). For instance, '*at Irangi (Tanzania) and Lake Victoria Nyanza, some specimens have black spots on the breast and abdomen while others are more like typical* biarmicus' (Hartert 1915).

This evident morphological variation among intergrades is what led the increase in the number of subspecies which were usually restricted to small geographical areas. Amongst others, these variations are represented by *F. Hierofalco tschusii* of the Tangier area of Morocco, *Falco lanarius capensis* (Cape region, South Africa), *F. lanarius*

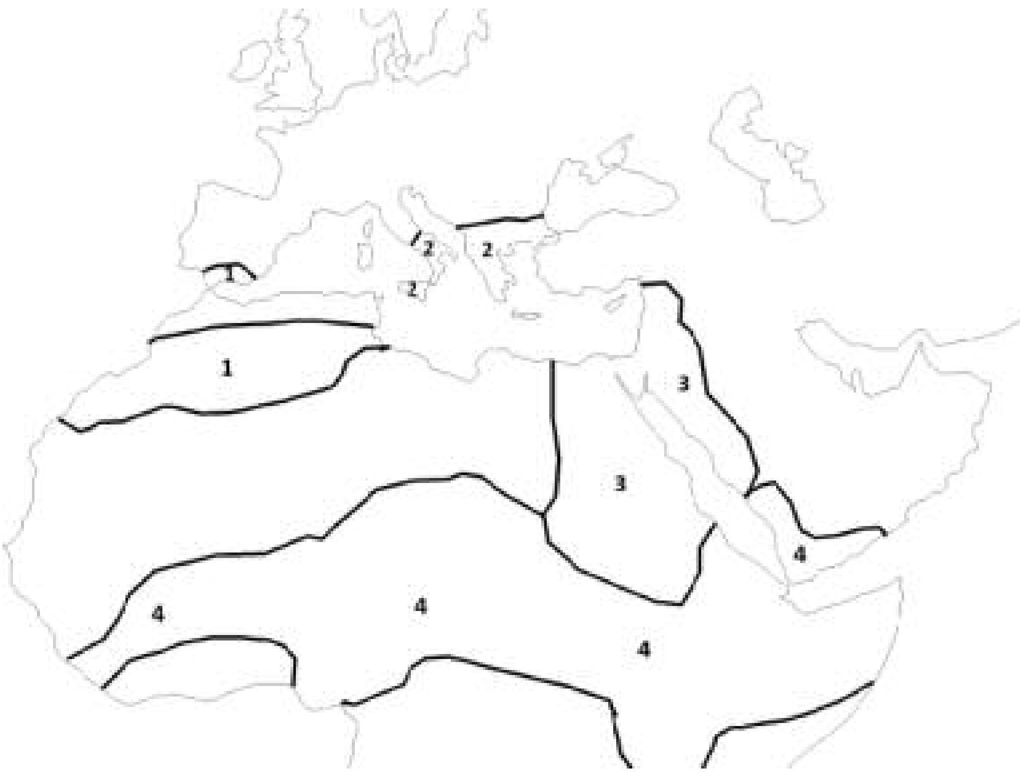


Figure 1.6 One of the first attempts to render on map the distribution of the Lanner falcon above the equator. 1- *F. b. erlangeri*, 2- *F. b. feldeggii*, 3- *F. b. tanypterus*, 4- *F. b. abyssinicus* (Simon 1965).

nubicus (Sudan) and *Falco b. orlandoi* (Sicily) (Kleinschmidt 1907, Schlegel 1843, Orlando 1957). Trischitta (quoted in Orlando 1957) supposed that three races were present in Sicily *erlangeri*, *feldeggii* and the new race *orlandoi* sp. inhabiting South-western Sicily only. In North and central Darfur, Lynes (1925) distinguishes Egyptian specimens of *tanypterus* from those of Ethiopia and South Sudan (*abyssinicus*) but considered birds from Darfur and arid zones to the east as intergrades with colour patterns similar to *tanypterus,* variable in size but somewhat larger than *abyssinicus*. In this way, after 10° N it is possible to find *abyssinicus* at least when the arid belt intergrades into savanna (Lynes 1925). This explanation was also plausible for Hartert (1915) who argues that the *feldeggii* race is the most distinct of the five races, while *biarmicus* and *erlangeri* are connected through *abyssinicus* and *tanypterus*. In 1833, the German zoologist Constantin W. L. Gloger (1803-1863) observed that birds found nearer the equator tended to be darker, where the environment is more humid (the so-called Gloger's rule). Thus, for the Lanner falcons, bright and pale colours along with the presence and variable shape of spots on the abdomen and flanks become important diagnostic features for the identification of subspecies between arid and '*humid*' environments (Table 1.9). The first most complete and detailed modern classification of Lanners was produced at the beginning of the twentieth century (Hartert 1912, 1915). In these two fundamental and comprehensive reviews, Ernst Hartert built up the first valid classification using trinomial nomenclature. Previously, Kleinschimdt (1901) had delineated all subspecies, including the new one *erlangeri*, and put them into the subgenus *Hierofalco*. Hartert recognized these subspecies and proposes the species *biarmicus* of Temminck as the nominate species, and all others as subspecies on the basis that *F. biarmicus* was the '*oldest name*' in this falcon group (Hartert 1902). Thus, the South African species are revised to their classifications (avoiding synonymous *cervicalis*, *chiqueroides* and so on), the *F. lanarius* of Schlegel was abandoned, but *F. feldeggii* remained as the European representative of the group. Two other forms were more clearly described than previously: *F. b. tanypterus* (from *F. tanypterus*) from North-eastern Africa (Reichnow 1900) and a new subspecies *F. b. abyssinicus* from the Eastern and Western tropical Africa (Neumann 1904). In 1902, Hartert wrote '*Diese 4 Formen stehen einander so nahe, dass man sie ohne Bedenken trinär benennen kann*' [These four forms are so close to each other that they may be described using trinomial nomenclature without hesitation]. The *erlangeri* was added in the last revision (Hartert 1912, 1915). Table 1.9 summarizes the main diagnostic features, including measurements, used for the identification of all subspecies. All data have been derived from a limited number of museum specimens but have been gathered from across the distributional range of all proposed subspecies. European *feldeggii* of the Balkans, Greece, Montenegro, Albania, Bulgaria, Herzegovina and S. Italy (Latium, Calabria, Apulia and Sicily), *erlangeri* of Morocco, Tunisia, Algeria, Libya and southern Spain, *tanypterus* of Egypt, '*Nubia*' and Arabia, *abyssinicus* of Ethiopia, Eritrea, Somalia and Togo and *biarmicus* of South Africa, Angola and limited areas of East Africa (Hartert 1912, 1915). One of the first comprehensive distribution maps for the Lanner falcon was made by Simon (1965) in which he spatially separates four races along the Palearctic ecozone and West and East Africa (Figure 1.6).

Falco biarmicus biarmicus

Unlike the other subspecies, no real doubt has ever been cast on the separation of *biarmicus* from other races purely on the basis of morphological features, particularly the unspotted abdomen and flanks (Layard and Sharpe 1875, Bree 1895, Whitaker 1905, Martorelli 1911, Langford 1912). A synonymous species name that was frequently used was *F. cervicalis* (Figure 1.7; Bree 1895). The syntype is an adult male from Cape region of South Africa preserved as a mounted skin at the RMNH (Temminck 1820-1839, Hoek Ostende *et al.* 1997). An other four specimens (three adult male and one adult female originally collected by H.B. von Horstok and J. Verreaux) were also used by Hermann Schlegel for the description of a presumed local subspecies named *F. lanarius capensis* (Schlegel 1862, Hoek Ostende *et al.* 1997). In fact, Temminck restricted this species to British Kaffraria (modern King Williams Town and East London districts) and the Cape of Good Hope regions (Temminck 1820-1839). As diagnostic morphological trait, he mentions the width of the orbital ring clearly depicted in a colour plate but makes no mention of moustaches (Temminck 1820-1839). Interestingly, while makes no comparisons with *Lanarius,* he also gives an account of a separate species not recognized by previous Authors and to which he gave the common name *Faucon biarmique* (Temminck 1820-1839). This subspecies was always closely linked to a specific geographical area hence the name South African Lanner falcon (Langford 1912, Finch-Davies 1920). The diagnostic plumage characteristic is the uniform and unspotted underparts with flanks showing a few black spots or short bars (Hartert 1915).

Falco biarmicus tanypterus

Schlegel (1862) identified two taxa: *Falco lanarius nubicus*, the so-called 'Nubian Lanner', and *F. tanypterus* although Bree (1859) considered *nubicus* and *tanypterus* as the same race. The type specimen and several and other individuals are conserved in the Berlin and Leiden Museums of Natural History (three adult females in the latter; Figure 1.8; Hartert 1912, Hoek Ostende *et al.* 1997). H. Schlegel also coined the name *Falco lanarius alphanet,* adopting the historical name of the Lanner used in falconry in the north-west Africa (Hartert 1912). The main morphological differences concern plumage colours (Schlegel 1843) and the subspecies is very similar to *F. b. erlangeri* but only a little darker and more frequently reaching larger sizes (Hartert

FIGURE 1.7 A female Lanner (*biarmicus* sp.) collected by J. L. L. Mund & L. Maire in the early nineteenth century described as *Falco lanarius cervicalis* Schlegel, 1851 (© and courtesy of the Museum für Naturkunde Berlin, photo M. Jurke).

1912). J. H. Gurney referred of an adult pair collected in Egypt in which the female was similar to the pale form of *feldeggii* and the male a little less darker than the *abyssinicus* race (Whitaker 1905).

Neumann (1904) was sceptical about a real separation between *erlangeri* and *tanypterus* due to the fact that, the individuals used for the characterization of this subspecies were drawn from a wide geographical area which covered Egypt and "*Nubia*", a large region reaching from southern Egypt to northern Sudan. In later examination of these museum specimens, darker individuals were described as *abyssinicus* race and paler ones as *tanypterus* (Neumann 1904). Thus, specimens which have been strictly ascribed as belonging to the subspecies *tanypterus* became more and more similar to the other subspecies of North-west Africa.

Falco biarmicus abyssinicus

The type specimen, an adult male, was collected at Turra Bolonka in Kollu, Shoa (a historical region of Ethiopia) in September 1900 and is now preserved in the Natural History Museum at Tring (Neumann 1904, Hartert 1915). According to Hartert (1915) *biarmicus* from southern Africa seems to merge into *abyssinicus* in East Africa. The latter is generally brighter, darker and has larger spots than the nominate race (Neumann 1904). Neumann (1904) mentioned also as a distinctive character the wide and undivided black frontal band. He thought that among specimens recognized as *tanypterus* (generally called Nubian Lanners) by previous Authors, including C. Bree, R. B. Sharpe and O. Kleinschimidt, there were several *abyssinicus*. In his opinion, this *tropicalische* form from the Dongola (northern Sudan) and Abyssinia regions (modern Ethiopia) is easily distinguishable from pale and less spotted Egyptian Lanners (Neumann 1904).

Falco biarmicus erlangeri

The subspecies was first described by C. von Erlanger and depicted by O. Kleinschmidt in 1898 but was not originally intended as a new form (Erlanger 1898, Elzen 2010). The first description (originally *F. Hierofalco erlangeri*) is based on several individuals (six males and five females) observed and collected in Tunisia and near Tangier in northern Morocco (Erlanger 1898, Kleinschmidt 1901, Hartert 1912, Elzen 2010). The type specimen is an adult female from Djebel Sidi Ali ben Aoun (Sidi Bouzid governorate, east-central Tunisia) captured on April 14th 1897 (Erlanger 1898, Neumann 1904, Elzen 2010). Kleinschmidt (1901) considered this new form plausible due to historical sources that mentioned a well distinguished type of falcon called *Alphanet*. The main characteristics of this race were plumage patterns of the head, which was pale in comparison with *feldeggii* sp., along with wing and tarsus measurements (Kleinschmidt 1901). Alexander Koenig also collected several adults, eggs and chicks while travelling in Tunisia and Algeria (Elzen 2010). Unlike the other subspecies, museums and private collections at the beginning of the twentieth century possessed a very impressive number of specimens relating to the *erlangeri* races, including several adult and immature birds and at least forty eggs.

Falco biarmicus feldeggii

Hermann Schlegel described this subspecies from five specimens, three from Dal-

Figure 1.8 A male Lanner (*tanypterus* sp.) classified as *Falco lanarius nubicus* Schlegel, 1862 and collected by W. Hemprich and C. G. Ehrenberg in the early nineteenth century in Sudan. Neumann (1904) studied these birds from the Berlin Museum collected in the so-called "Nubia" and describe the new form *abyssinicus* more bright in colour than the pale *tanypterus* (© and courtesy of the Museum für Naturkunde Berlin, photo M. Jurke).

matia (the exact locality is unknown) and two from Greece (Schlegel 1843, Mlíkovský 2005a). Two of the three syntypes collected in 1829 in Dalmatia are deposited in NMP (National Museum of Prague), the third being donated or sold by Feldegg to RMNH prior to 1844 (Schlegel 1843, Hoek Ostende *et al.* 1997, Mlíkovský 2005a). Further Greek specimens were added as proof of the subspecies but not included in the final type series (Schlegel 1843, Mlíkovský 2005a). Curiously, prior to Schlegel, H. Schinz used the name *Falco feldeggii* as synonymous with *Falco pallidus*, modern *Cir-*

cus macrourus Gmelin, 1770) (Sharpe 1874). In deference to the origin of the specimens, this race was also called Greek Lanner and it also obtained subspecies status as *Falco lanarius græcus* Schlegel (Bree 1895). This subspecies (also as *F. b. feldeggii*) was considered as the race which also inhabited Tunisia, Egypt and *Nubia* or Sudan (Bree 1895, Whitaker 1905). Nevertheless, Schlegel does not seem certain of the status of the *græcus* subspecies, a name under which he seems to have assembled specimens of *feldeggii* and *tanypterus* (Hartert 1915).

Phylogenetic relationships among subspecies

Nittinger *et al.* (2005) used the variable sections of the *mt* genome to elucidate the phylo-geographic history of the Lanner falcon. First of all, the Lanner falcon seems to have had a fundamental role in the evolution of the *Hierofalco* complex. In particular, a sub-Saharan origin of Hierofalcons seems probable, given the large number of haplotypes of Lanners found in the Afrotropics (Nittinger *et al.* 2005, 2007). In addition, a close relationship exists between these haplotypes suggesting a rather recently radiation of four Hierofalcons (Gyr-, Laggar, Lanner and Saker falcons) according to results previously obtained from nucleotide sequences of the *cytb* gene (Wink *et al.* 2004). Three main haplotypes were identified and it appears that these morphologically distinct species are not clearly differentiated genetically with respect to neutral marker sequences (Nittinger *et al.* 2005). In fact, the main haplotype III is shared by all Hierofalcons species, the *F. cherrug* specimens of cluster II are more closely related to the *F. biarmicus* ones (clusters I and II) than to the remaining haplotypes of *F. cherrug* in cluster III (Nittinger *et al.* 2005). The paraphyly of Lanner and Saker falcons was also found in a previous analysis of *cytb* sequences (Wink *et al.* 2004). The NJ (neighbour-joining) tree identified a clade (A) which contains all four species and a clade (B) which consists only of Saker and Lanner individuals (Nittinger *et al.* 2005; see chapter 10). Thus, the *Hierofalco* complex is an assemblage of morphospecies not yet differentiated and should properly be considered a superspecies (Nittinger *et al.* 2005). Accordingly, the Peregrine falcon seems also to be a recently diverged species, and haplotypes were similarly found to be broadly shared across its subspecies (White *et al.* 2013).

Intraspecific variation in phenotypic characters can occur rapidly through processes associated with adaptation to local environments (Merilä and Crnokrak 2001, Zink 2004). Nevertheless, insufficient time for the accumulation of genetic differences can tend to obscure phylogenetic relationships among subspecies (Zink 2004, Hull *et al.* 2010). In fact, none of the taxa (species/subspecies) corresponds to a distinct *mt*DNA haplogroup and none of the four *Falco* species appears as monophyletic (Nittinger *et al.* 2007). This lack of monophyly could be due to incomplete sorting of *mt*DNA lineages from a polymorphic ancestral gene pool or it could be

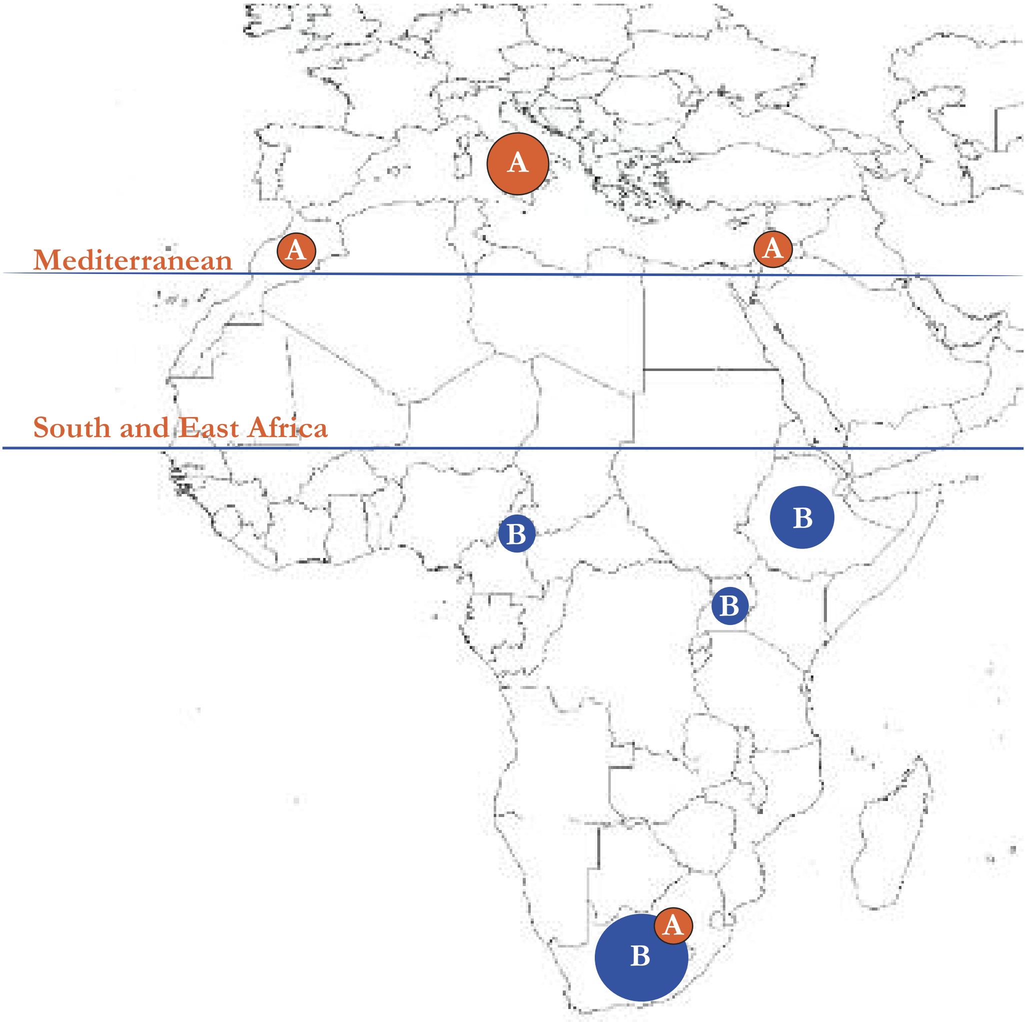


FIGURE 1.9 Frequencies of A and B haploclades in populations of *F. biarmicus* (Nittinger *et al.* 2005, 2007). Circles are scaled to reflect number of individuals examined. Haplotypes: South and East Africa (A = 3, B = 20) - Ethiopia: H-46 (n = 3), Cameroon: H-47 (n = 1), Uganda: H-53 (n = 1), South Africa: H-45 (n = 1), H-48 (n = 1), H-49 (n =1), H-50 (n = 1), H-51 (n = 1), H-52 (n = 1), H-54 (n = 7), H-55 (n = 1), H-56 (n = 1), H-57 (n = 2), H-59 (n = 1). Mediterranean region (A = 7, B = 0) - Morocco: H-62 (n = 1), Italy: H-63 (n = 2), H-69 (n = 1), H-53 (n = 1), Israel: H-60 (n = 1), H-61 (n = 1).

due to a process of hybridization (Nittinger *et al.* 2007).

Another analysis of mitochondrial *mt*DNA sequences revealed two main clades among Lanner subspecies which showed that the subspecies are not randomly distributed (Nittinger *et al.* 2005). Clade A comprises *biarmicus*, *erlangeri*, *feldeggii*, *tanypterus* races whereas in clade B only *biarmicus* and *abyssinicus* occur (Figure 1.9). Afro-tropical representatives form a separate cluster except for one individual from

East Africa, whereas Palearctic individuals are apparently dispersed (Nittinger *et al.* 2007). In fact, twenty different haplotypes occurred (*n* = 29 individuals) and most of them form the centre of the maximum parsimony network of control region (represented entirely by *biarmicus* sp.), fifteen possess a private haplotype (locus MsFp01: alleles 152 and 156) and those of *abyssinicus* are derivatives of the centre (Nittinger *et al.* 2005). Thus, (a) nominate *biarmicus* is the only race belonging to both groups, (b) overall *abyssinicus* is directly derived from *biarmicus*, (c) Ethiopian (E Africa) *abyssinicus* specimens share the same haplotype (H-46) separated by a single substitution with the individual from Cameroon (E Africa; Figures s1 and s2), (d) the specimen from Uganda is clearly separated from the main cluster, and (e) current contacts among *erlangeri* and *abyssinicus* in West Africa (Mauritania, Mali, Niger, and Chad) and *tanypterus* and *abyssinicus* (South Sudan and Yemen) occurred after this process of differentiation.

F. b. feldeggii haplotypes linked the centre with the third main cluster constituted mainly by Saker (*n* = 6) and Gyrfalcon (*n* = 5) individuals (Nittinger *et al.* 2007). Interestingly, *feldeggii* haplotypes from the Italian mainland (Tuscany and Apulia) are separated by four substitutions with a specimen from Sicily (the only one that possesses main haplotype III) and by a single substitution with Moroccan *erlangeri* (Nittinger *et al.* 2005). This structure suggests that (a) *tanypterus* from Israel and *erlangeri* are not directly connected, (b) the Italian mainland population is more close related with Moroccan *erlangeri* than the Sicilian population which is more closely aligned with *tanypterus*, (c) *feldeggii* from the Italian mainland is the only race directly connected with *biarmicus* A group and Saker individuals, as well Laggar falcons.

Finally, two *tanypterus* from Israel are derivatives of the main haplotype III (the same as *feldeggii* and Saker) and are not directly connected to the other *F. biarmicus* haplotypes (Nittinger *et al.* 2005). According to the genetic data, these two individuals could be considered as putative *F. biarmicus*/*F. cherrug* hybrids or descendants of hybrid parents (Nittinger *et al.* 2007). Archaeological excavations near the Sea of Galilee revealed the concomitant presence of the Saker and Lanner among fossils of the Late Pleistocene (Simmons and Nadel 1998). Thus, in contrast to the current distribution of these falcons (whereby Saker falcon is a very rare migrant and Lanner falcon a rare breeding species), Israel has in the past been a contact area between which are now distinct populations. Two further point suggest links between *feldeggii* and *tanypterus*: (a) prior to 1950 both subspecies bred in Israel (Mendelssohn 1972) and (b) tracked *tanypterus juveniles* from Israel tended to move northwards towards and inside central and western Turkey, the region formerly occupied by the *feldeggii* race (Hatzofe 2001).

Overall at least four differentiated groups were observed: Sakers, Gyrfalcons and two groups of Lanners where *F. cherrug* is clearly separated from *F. biarmicus* and *F. rusticolus* (Nittinger *et al.* 2007). The analysis of variation of nuclear microsatellites

FIGURE S1 Dorsal view of an adult male *F. b. abyssinicus* captured in Burkina Faso (Western Africa). © and courtesy of Marco Pavia.

FIGURE S2 An adult *F. b. abyssinicus* in flight over Gonder, in the Simien National Park, Ethiopia (Eastern Africa). © and courtesy of Bruno D'Amicis.

also identified two macro geographic areas for the Lanner groups, one comprising *F. b. biarmicus* and *F. b. abyssinicus* from South and East Africa (SEA, *n* = 25), and the other containing the remaining three subspecies (*F. b. erlangeri*, *F. b. tanypterus*, and *F. b. feldeggii*) from the Mediterranean region (MED, *n* = 8; Figure 1.9) (Nittinger *et al.* 2007). The presence of two genetic groups corresponding with geographic regions avoids a high level of homoplasy (Nittinger *et al.* 2007).

The effective number of alleles was highest (6.0) in the Mediterranean group. Overall, the number of alleles detected was 33 and 39 for MED and SEA groups respectively, the effective number of alleles was 6 (MED) and 2.9 (SEA), and the expected average heterozygosity 0.833 (MED) and 0.653 (SEA; Nittinger *et al.* 2007). The heterozygosity is the presence of different alleles at one or more *loci* on homologous chromosomes and it can therefore be used as a general indicator of the amount of genetic variability (Höglund *et al.* 2007). This high genetic diversity is possibly due to the admixture of lineages from different *refugia* that gave rise to a hybrid zone with Saker falcons (Nittinger *et al.* 2007, Provan and Bennett 2008). In fact, in the Pannonian region the admixture analysis identified 19% of putative hybrids or hybrid descendants (Nittinger *et al.* 2007). This explanation is also possible for current wild populations of Lanner and Saker falcons in Bulgaria where hybridizations should be also possible (Iankov 2007).

In summary, the Lanner falcon possesses private microsatellite alleles and the South African population forms two compact branches in the NJ tree, while the Mediterranean individuals are distributed in other branches of the tree (Nittinger *et al.* 2007). As expected from Figure 1.9, the Sahara desert played a fundamental role in this process of diversification through the geographical separation of the main group (A and B; Figure 1.9) (Guillaumet *et al.* 2008, Gonçalves *et al.* 2012, Korrida and Schweizer 2013). Section 3.5 integrate these phylogenetic results with fossil evidence (*cf.* 1.1), phenotypic data (*cf.* 2.3), and potential distribution by macro-areas in a comparative framework (*cf.* 3.4).

Chromosome structures

The avian karyotypes are highly conserved at the molecular level and species belonging to the genus *Falco* have lower diploid chromosome numbers ranging from 40 to 54, comprising 7-11 pairs of large- and medium-sized, mostly acrocentric chromosomes and around 13-16 pairs of microchromosomes (Nishida *et al.* 2008). Along with the Common Kestrel and the Red-necked falcon, the Lanner falcon lacks the metacentric pair 1 and has one additional pair of equal sized acrocentrics (Belterman and de Boer 1984). In addition, Lanner and Red-necked falcons both have a structural heterozygosity with the presence of short arms in pair 9 (Belterman and de Boer 1984). Generally, conserved avian karyotypes with a small number of macro-

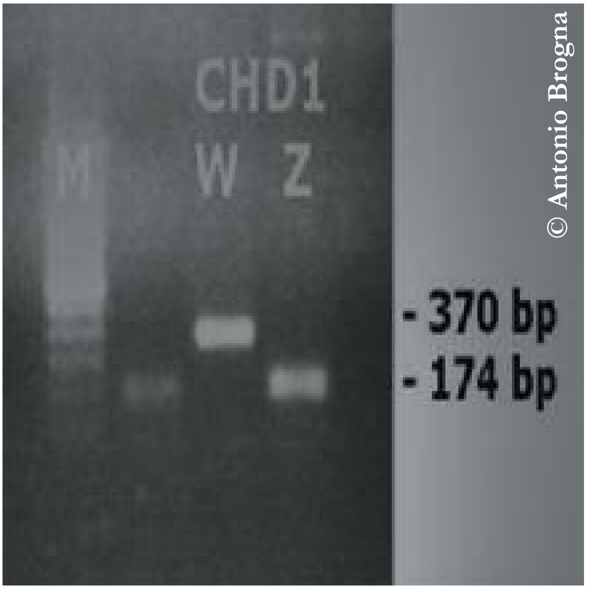


Figure 1.10 Image of an electrophoretic run in a 2% agarose gel of CHD1 gene on W and Z of *F. biarmicus feldeggii* (© and courtesy of A. Brogna).

chromosomes and a large number of microchromosomes denotes an ancestral state.

The ancestral karyotype of the genus *Falco* was probably 2*n* = 52 or 54, comprising all acrocentric macrochromosomes including Z and W chromosomes and acrocentric microchromosomes (Belterman and de Boer 1984, Nishida *et al.* 2008). This fact is evident for the Gyrfalcon and Common Kestrel (2*n* = 52) and even more so for the Lanner falcon (2*n* = 52 or 54; Schmutz and Oliphant 1987, Nishida *et al.* 2008). Among the *Hierofalco* species, these findings support the early appearance of the Lanner suggested by mitochondrial DNA analysis (Nittinger *et al.* 2005).

The CHD1 gene (Chromo-Helicase-DNA binding protein), conserved on an avian W chromosome, also allows determination of sex in most avian species (Ito *et al.* 2003). As with other large falcons, the Lanner exhibits reversed sexual size dimorphism (RSD) but sexing nestlings properly before attaining asymptotic weights is not easy, especially in the earliest stages of their development (Hurley *et al.* 2007). Genomic DNA was extracted from blood samples taken from wild Lanner falcon chicks (*feldeggii* race) in eastern Sicily (Brogna *et al.* 2005). The sexing method based on intronic length polymorphism gave for the gene CHD1W a 370 bps amplified product, while a 174 bps fragment was obtained for CHD1Z. Female Lanner falcons shows both amplified products, while males show only a 174 bps fragment (Brogna *et al.* 2005; Figure 1.10).

Polymorphism at MHC genes

Genes of the major histocompatibility complex (MHC) play an essential role in the adaptive immune response by coding for molecules that recognize and present antigenic peptides to T lymphocytes (Gangoso *et al.* 2012). There are two remarkably different patterns of MHC class I and MHC class II (*loci*) variation among the genus *Falco*, where kestrels display an extremely high MHC variability and other falcons low intra- and interspecific diversity (Alcaide *et al.* 2007, Gangoso *et al.* 2012). In fact, the number of highly similar aminoacid sequences found at the MHC class II B (exon 2) of falcons ranged from one to three per species (Gangoso *et al.* 2012). Accordingly, the Lanner falcon shows low polymorphism of MHC genes with only two different alleles per locus (Na) and an average number of nucleotide differences between alleles of 2.00 (Alcaide *et al.* 2007). Nevertheless, this MHC impoverishment has not prevented the ecological radiation of falcons or their successful colonization of most habitats worldwide and MHC sequences correspond to the mitochondrial DNA-based phylogeny of this genus (Wink *et al.* 2010, Wink 2011, Gangoso *et al.* 2012). Nittinger *et al.* (2005) suggested that Hierofalcons radiated much more recently and in fact the high similarity among the MHC presume a common ancestor for these birds but with already-depleted and slow-evolving MHC. The maintenance of polymorphic low levels is potentially associated with a high innate efficiency of the immune system in falcons by virtue of specific rather than extensive MHC repertoires (Wegner *et al.* 2007, Gangoso *et al.* 2012).

Hybrids

Hybridization is a significant additional threat for species which are already endangered and could potentially even lead to their eventual extinction (Fleming *et al.* 2011). Nevertheless, hybridization provide new material for the speciation process and it is often associated with rarity (Newton 2003). Mixed pairing in birds is more common where one of the two parental species is rare due to the scarcity of conspecifics (Randler 2006). Indeed, hybridization is not uncommon in zones where Sakers encounter Lanner falcons or Gyrfalcons (Nittinger *et al.* 2007). Nevertheless, Boev and Dimitrov (1995) reported a recent case of a presumed Lanner × Saker individual in Bulgaria but neither microsatellite nor *mt* analyses indicate hybridization (Nittinger *et al.* 2007). On the other hand, in Israel, another zone of contact between these falcon species, two specimens of *tanypterus* sp. could be considered as putative hybrids or hybrid descendants (Nittinger *et al.* 2007).

Due to the genetic affinities among species of the *Hierofalco* complex, hybrids from within this group exhibit full fertility, presumably over indefinite generations (Heidenreich *et al.* 1993, Nittinger *et al.* 2005) and hybridization has been seen to be easily accomplished in various parental combinations giving rise to fertile offspring (Heidenreich *et al.* 1993).

Thus, F_1 hybrids are fully viable and in turn can produce F_2 hybrids or back crosses to one or other parent species (first B_1 and second B_2 generation backcrosses; Heidenreich *et al.* 1993). It seems that hybrids with Laggar falcon, however, are only partially fertile (McCarthy 2006). Although a certain genetic distance exists between the Lanner and Peregrine falcons, hyridization has been reported to occur both in

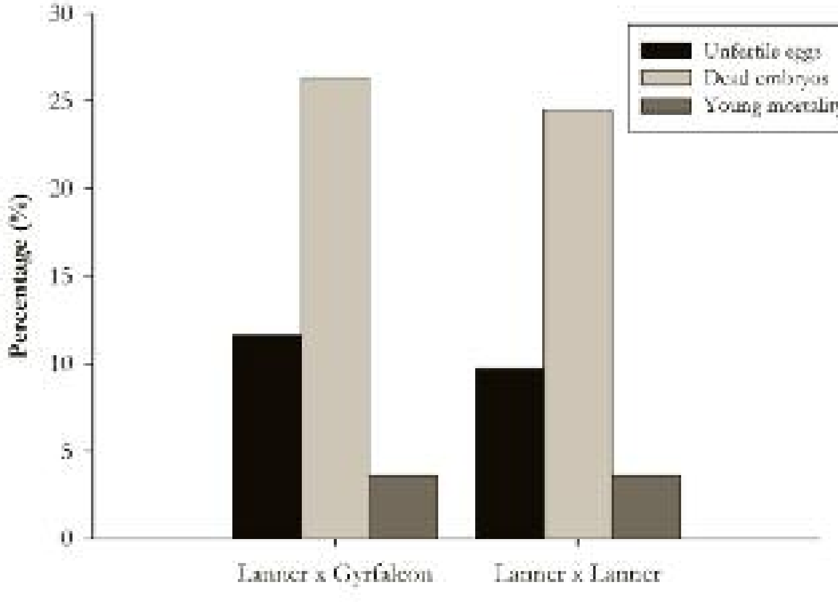


FIGURE 1.11 Failure percentages of captive hybridization among female Lanner and male Gyrfalcon (*candicans* sp.) and captive purebred Lanner falcons. Total eggs laid: 42 (hybridization) and 41 (purebred) (Cade *et al.* 1977, Heidenreich *et al.* 1993).

captivity and in the wild but with the resulting male hybrids only partially fertile (McCarthy 2006).

Nittinger *et al.* (2007) suggest a minor role of admixture due to strong selection pressures against the survival of intermediate phenotypes. In addition, Wink (2011) predicted a very low impact of hybrids on the health of Peregrine and Saker populations by genetic swamping. Nevertheless in the last few decades, a growing number of escaped hybrids represented a continuous source of interspecific gene flow and introgression (Fleming *et al.* 2011). As observed in southern Scandinavia, the considerable gene introgression from the captive breeding population (from both indigenous and exogenous sources) altered the genetic composition of local Peregrine populations (Jacobsen *et al.* 2008). In the UK as well as in Germany and Austria, a high number of captive Lanner falcons and Lanner-like hybrids were observed or recorded as having escaped into the wild (10% of escapes in UK from 1986 to 1994; Fleming *et al.* 2011). Captive hybrids produced by artificial insemination have similarly low failure rates when compared with pure-bred captive birds (Figure 1.11; Cade *et al.* 1977, Heidenreich *et al.* 1993).

Hybrids may also be bred in genetic mixture of 50-50, 62.5-37.5, 75-25, or in combination of more than two species (Table 1.10). They varied in an unpredictable

FIGURE 1.12 The Lanner-like male (back and frontal view) paired with a female Peregrine in the Edinburgh area of Scotland. Jesses revealed it as an escaped bird. This mixed pair produced two (2013) and three (2014) young (F. Germi pers. comm.) (© and courtesy of F. Germi).

way due a mixture of characteristics and this mix is not consistent (i.e. individuals are dissimilar in spite of the same parental species; Eastham and Nicholls 2005).

Unfortunately, phenotypic traits such as wing, tail and tarsus lengths are not reliable measurements characteristics for the identification of hybrids but they do reveal F_1 hybrids share more similarities with their paternal than their maternal progenitors (Eastham and Nicholls 2005). For example, a male bird observed several times in Bavaria, paired with a local female Peregrine, was identified as Lanner × Peregrine by Wink (2011) and Peregrine × Red-naped Shaheen (Robitzky 2013). Researchers resorted to genetic analysis for the correct identification of a male hybrid in Sussex classified as a [(Gyrfalcon- × Prairie falcon) × Peregrine] hybrid based on morphological features, but it was actually turned out to be a three-way mixture [(Gyrfalcon- × Saker) × Peregrine](Everitt and Franklin 2009).

Since 2012, a mixed pair was observed nesting in the Edinburgh area. A local female Peregrine mated with a male falcon (wearing jesses) with a plumage pattern very close as plumage patter very close to a pure Lanner falcon (Figure 1.12; F. Germi pers. comm.) and the pair proved productive over the subsequent

× **Saker Falcon** (female)
× **Laggar Falcon**
(Laggar × Lanner) × Peregrine
× **Barbary Falcon** (male)
× **Peregrine Falcon**
(Peregrine × Gyr- × Saker) × Lanner
(Barbary/Gyr) × (Peregrine/Lanner)
× **Gyrfalcon** (male)
[(Saker × (Barbary × Gyrfalcon)]
(Barbary/Gyr) × (Gyr/Lanner)

Table 1.10 Possible hybrids produced among pure species or three-way and four-way hybridizations (McCarthy 2006).

two years producing five young in total. Presumably, this male should possess a variable percentage of admixture.

The main characteristic that unites all these cases is that they occurred far outside of the usual distribution range of the Lanner falcon. It therefore seems that, altough environmental conditions are clearly unfavourable for all Lanner races, these could be overcome by more adaptable hybrid birds. A certain number of *erlangeri* sp. have also been observed arriving in Iberia from Morocco via Gibraltar but, in spite of the availability of what would seem to be more suitable and hospitable habitats, no recent breeding attempts have been recorded. Presumably in northern Europe, captive pure-bred or hybrids birds were unable to overcome the disadvantageous effects posed by the availability habitats as suggested by Nittinger *et al.* (2007).

On the other hand, it seems likely that some gene flow will take place between different subspecies where they reach the same large areas (*abyssinicus*/*erlangeri* in Sahelian zones for example). Could this also be true for escaped or released captive birds? For instance, a one year old bird has been observed flying with a trained falcon in the Hottentots Holland Mountains in the Western Cape Province of South Africa (MacLeod *et al.* 1951). In addition captive birds should be able to compete with the local wild race, as reported in Shabita (El Rub'al Khali, Saudi Arabia) where an escaped falconer's bird with jesses was hunting wagtails (Pambour and Al Karrairy 1991). As Fleming *et al.* (2007) state '*the extent of any human-induced genetic introgression into wild populations arising from escaped captive-bred falcons remains to be evaluated*'.

Chapter 2.
Structure and functions

2.1 Osteology

The genus *Falco* is characterized by a highly distinctive bone morphology (Guerra *et al.* 2013). Some traits are diagnostic such as the humerus with a strongly marked *crista deltoidea*, a powerful *processus flexorius,* and the absence of *procoracoid foramen* in the coracoid (Guerra *et al.* 2013). Characteristics such as these, are responsible for the differences among species especially with regard to absolute size and proportions (Louchart 2002, Guerra *et al.* 2013). Table 2.1 shows a range of measurements taken from Lanner falcon bones, although from only a small number of individuals.

Béla Solti authored a paper devoted solely to the bones of Lanner falcons (Solti 1981b) as well as two others on comparative aspects with the bones of the Gyrfalcon (Solti 1980) and the Saker falcon (Solti 1981a). A review of current knowledge and a comparative analysis with the Peregrine along with additional data, was made more recently by Louchart (2002; see Table 2.4). Bones belonging to Lanner and Sakers share many morphological similarities but these falcons should be separated due to

FIGURE 2.1 Lanner falcon skull (lateral view). © and courtesy Wouter van Gestel (Experimental Zoology group, Wageningen University - *www.skullsite.com*).

	Label (subsp., sex)	Ref. number	Collection
1	*erlangeri*, male		Inst. Paleoanatomie, Univ. Müchen
2	*biarmicus* no ssp., female		Inst. Paleoanatomie, Univ. Müchen
3	*feldeggii* (?), male		Inst. Paleoanatomie, Univ. Müchen
4	*feldeggii*		Natural History Museum, Budapest
5	*biarmicus* no ssp, male	S/1976.60.5	Natural History Museum, London
6	*abyssinicus*, female	S/1956.14.6	Natural History Museum, London
7	*biarmicus* no ssp.	S/1996.45.1	Natural History Museum, London
8	*biarmicus* no ssp.	S/1962.20.1	Natural History Museum. London
9	*biarmicus* no ssp.	IPH 699	Muséum Nat. Hist. Naturelle, Paris
10	*biarmicus* no ssp.	IPH 1531	Muséum Nat. Hist. Naturelle, Paris

Table 2.1 Specimens of the Lanner falcon used for bone measurements. Individuals 1-4 used by Solti (1981b), 7-10 by Louchart (2002). Specimen 5-6 measured by both Authors. Specimen no. 1 was probably collected in Morocco and no. 6 in the Afrotropics.

marked differences among absolute measurements (Solti 1981b). In fact, the Lanner is clearly the smaller species and no significant overlap occurred between the other species, even when smaller individuals of Saker falcon were included (see Figure 2.3; Solti 1981b). On the other hand, bone measurements and their index values of the Lanner falcon could lead to misidentification when compared with those of the Peregrine (Solti 1981a, b; Louchart 2002; Table 2.4).

Tables 2.2 and 2.3 summarize measurements and osteological indexes respectively for the main bones of the Lanner falcon. According to Solti (1981b) four traits can be considered indicative the species:

• a narrower and more elongated sternum
• a longer *Crista Marginis ventralis*
• a larger cranial epiphysis of the coracoids
• a larger sized *Crista lateralis humeri*

The humerus shows a deeper and sometimes pneumatized *incisura capitis*, the distal tibiotarsus have a trapezium-like *trochea cartilaginis tibialis* and an elongated and more evident tip laterally to the *condylus lateralis* (Bedetti and Pavia 2013). All of these skeletal traits suggest more manoeuvrable flight as well as the length of the third and fourth toes being adapted for catching avian prey (Solti 1981b).

The contour line of the cranium is usually smoothly curved (average length/width index = 1.57) as well the Saker (1.55) although some specimens can show a certain similarity in shape with the cranium of the Peregrine (1.60; Figures 2.1 and 2.4; Solti 1981b). There is less overlap with the Saker falcon regarding the absolute dimensions of the Lanner falcon cranium, which is noticeably smaller (Solti 1981b). Superciliary arches are widely bent, even the bone itself is wide, and the width of the frontal

Bones	Male	Female
Coracoideum		
cor 1	42.6 - 45.4 (n = 2)	46.0 - 48.6 (n = 2)
cor 1b	38.0 - 41.6 (n = 4)	42.3 - 44.1 (n = 2)
cor 4	17.2	16.0 - 19.0 (n = 2)
cor 4b	15.0	18.5
cor 5	2.8	3.10 - 4.70 (n = 2)
cor 6b	4.30 - 4.70 (n = 7)	4.90 (n = 2)
Humerus		
hum 1	72.2 - 75.6 (n = 3)	83.1 - 84.1 (n = 5)
hum 2		18.5 - 19.0 (n = 4)
hum 2b	23.0 - 26.0 (n = 5)	23 - 26 (n = 5)
hum 4	13.3 -	15.4 - 15.7 (n = 3)
hum 6b	6.0 - 6.3 (n = 3)	6.3 - 7.0 (n = 3)
Radius		
rad 2	5.5 -	5.7 - 6 (n = 2)
rad 3	3.9 -	4 - 4.5 (n = 2)
rad 4	7.0	7.2 - 7.6 (n = 4)
Carpometacarpus		
cmc 1	51.4 - 54.0 (n = 2)	58.4 - 58.7 (n = 4)
cmc 2	13.5 -	14.6 - 15.5 (n = 2)
cmc 3		5.7 - 5.8 (n = 2)
cmc 4	9.0 -	9.4 - 9.9 (n = 2)
cmc 6b	3.0 - 3.1 (n = 2)	3.5 - 3.9 (n = 3)
Femur		
fem 2	11.2 -	12.2 - 12.6 (n = 2)
fem 3		7.7 - 8.0 (n = 2)
fem 6b	5.2 - 5.6 (n = 2)	5.4 - 6.5 (n = 4)
fem 7	5.0 - 5.5 (n = 5)	5.0 - 5.5 (n = 5)
Tibiotarsus		
tbt 1	77.3 - 80.4 (n = 2)	83.7 - 87.0 (n = 4)
tbt 2		10.3 - 11.5 (n = 2)
tbt 2b	13.3 - 13.7 (n = 3)	13.3 - 13.7 (n = 3)
tbt 3		11.6 - 12.6 (n = 2)
tbt 4		11.2
tbt 5		8.5
tbt 6b	4.60 - 4.90 (n = 2)	5.4
Tarsometatarsus		
tmt 4	11.2 - 11.6 (n = 2)	12.7 - 13.0 (n = 4)
tmt 5		8.8
tmt 5b	10.7 - 11.7 (n = 4)	10.7 - 11.7 (n = 4)
tmt 6b	4.4 - 4.5 (n = 2)	5.0 - 5.4 (n = 2)

Table 2.2 Ranges of bones measurements of the Lanner falcon from Solti (1981b) and Louchart (2002). Measurements follow the classification used in Mourer-Chauviré (1975) and Louchart (2002): 1 - Total length, 2 - width of the proximal epiphysis, 3 - thickness of the proximal epiphysis, 4 - width of the distal epiphysis, 5 - thickness of the distal epiphysis, 6b - minimum width of the diaphysis.

Bones	Rates
Coracoideum (cor 1/cor 6b)	9.35 - 10.3 (n = 5)
Humerus (hum 1/hum 2)	4.15 - 4.41 (n = 5)
Humerus (hum 1/hum 2b)	3.12 - 3.32 (n = 5)
Humerus (hum 1/hum 4)	5.06 - 5.74 (n = 5)
Humerus (hum 1/hum 6b)	11.51 - 12.7 (n = 5)
Humerus (hum 2b/hum 2)	1.31 - 1.41 (n = 5)
Radius (rad 4/rad 2)	1.21 - 1.33 (n = 4)
Carpometacarpus (cmc 1/cmc 2)	3.75 - 4.13 (n = 5)
Carpometacarpus (cmc 1/cmc 4)	5.71 - 5.93 (n = 5)
Carpometacarpus (cmc 1/cmc 6b)	14.19 - 16.28 (n = 5)
Tibiotarsus (tbt 1/tbt 2b)	5.9 - 6.67 (n = 4)
Tibiotarsus (tbt 1/tbt 4)	6.68 - 8.42 (n = 4)
Tibiotarsus (tbt 1/tbt 6b)	15.86 - 17.39 (n = 4)

Table 2.3 Osteological rates of main bones of the Lanner falcon from Solti (1981b) and Louchart (2002).

pars nasalis is larger than in the Saker (Solti 1981b). The mandible measured on average 45.1 mm (range: 43.3-46.9) and its shape is again similar to the Saker, particularly the mandibular foramen (Solti 1981b). The Lanner falcon cranium shows a single, central optic foramen (max. diameter = 3.59 mm) that probably reflects the size and position of the optic chiasm (Type 2; Hall *et al.* 2009). In accordance with activity patterns and, the length of the optic foramen, the orbit diameter (23.22 mm) and the inner diameter of sclerotic ring (11.28 mm) are consistent with values for other diurnal bird species (Hall *et al.* 2009). The shape of the quadrate bone of the Lanner falcon is intermediate between Saker and Peregrine, and the upper articulation surface for the mandible shorter than Saker but wider (Solti 1981b).

The furcula bone is extremely strong with a wide *caudal processus* and the two tubercles (*coraeoidaIe* and *scapulae*) have the same height (Solti 1981b). The distance from the cranial epiphysis to the *processus scapularis* and *corpus coracoidei* is greater than that of the Saker and the coracoid (including the *crista coracoidei)* is narrower (Solti 1981b). The medial border of the cranial epiphysis of the scapula near the acromion is straight or slightly concave (Solti 1981b). The sternum is quite different from that of the Saker, being narrower and more extended (Solti 1981b). The ventro-caudal margin pygostyle near the cranial tip is slightly bent (Solti 1981b).

The *crista lateralis* of the humerus is stronger and larger than that of the Saker but the length/width index values clearly separate the Lanner from other Hierofalcons (Figure 2.3; Solti 1981b). The radius is wider than that of the Saker and the width of distal epiphyse and the degree of curved part of the bone are also larger (Solti 1981b). Also, the ulna is larger with a wider distal epiphyse and *olecranon* (the latter

Bones	Female Lanner	Male Peregrine
Coracoideum	Short 1 and 2 and low 1/6b ratio	Short 1 and 2 and low 1/6b ratio
Humerus	Short 1 and very large 6b	Long 1 and very large 4 and 6b
Radius	Very short 2	Very long 3
Carpometacarpus	Short 1, very long 3, very short 4	Very long 1, long 3, large 6b
Tibiotarsus	Short 1, very short 2, small 6b	Very long 2, very long 3

TABLE 2.4 Main differences outlined by Louchart (2002) among the measurements and index values from diagnostic bones of female Lanners and male Peregrine falcons.

is a large, thick, curved bony eminence situated at the proximal end of the ulna; Solti 1981b).

The comparative analysis made by Solti (1985) revealed some significant differences between three species of Hierofalcon (Lanner, Saker and Gyrfalcon) and also with the Peregrine Peregrine (Figure 2.2). Overall, the Lanner appears to be the smallest species based on the subdivision of the skeleton into three main parts (thorax, wing and leg; Figure 2.2). Nevertheless, the wing/thorax ratio (2.53) is less than the Saker but more than the Gyrfalcon and the leg/thorax ratio (1.86) is the greater (Solti 1985). The Saker is the most slender falcon with ratios similar to the Lanner

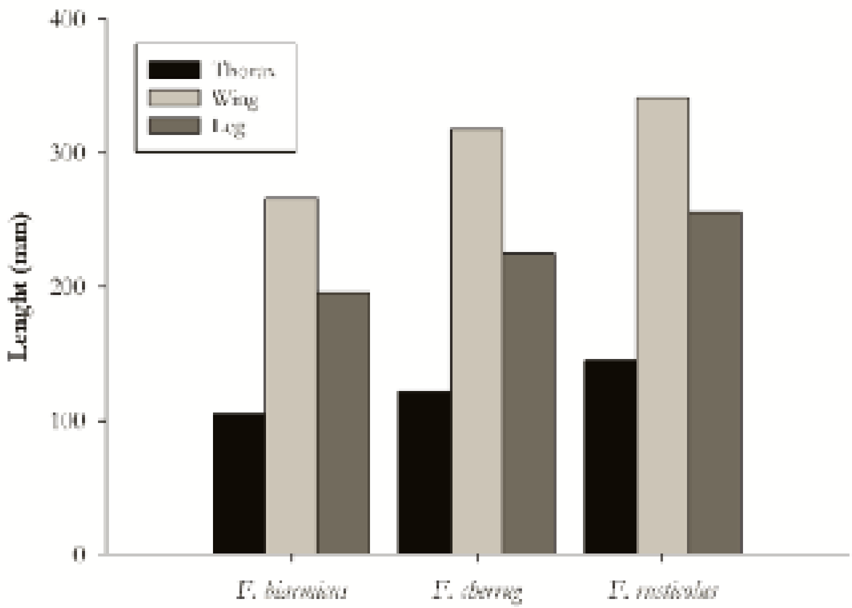


FIGURE 2.2 Mean lengths of thorax (coracoideum and sternum), wing (humerus, ulna, carpometacarpus, digits) and leg (femur, tibiotarsus and tarsometatarus) of the Lanner, Saker and Gyrfalcon (Solti 1985).

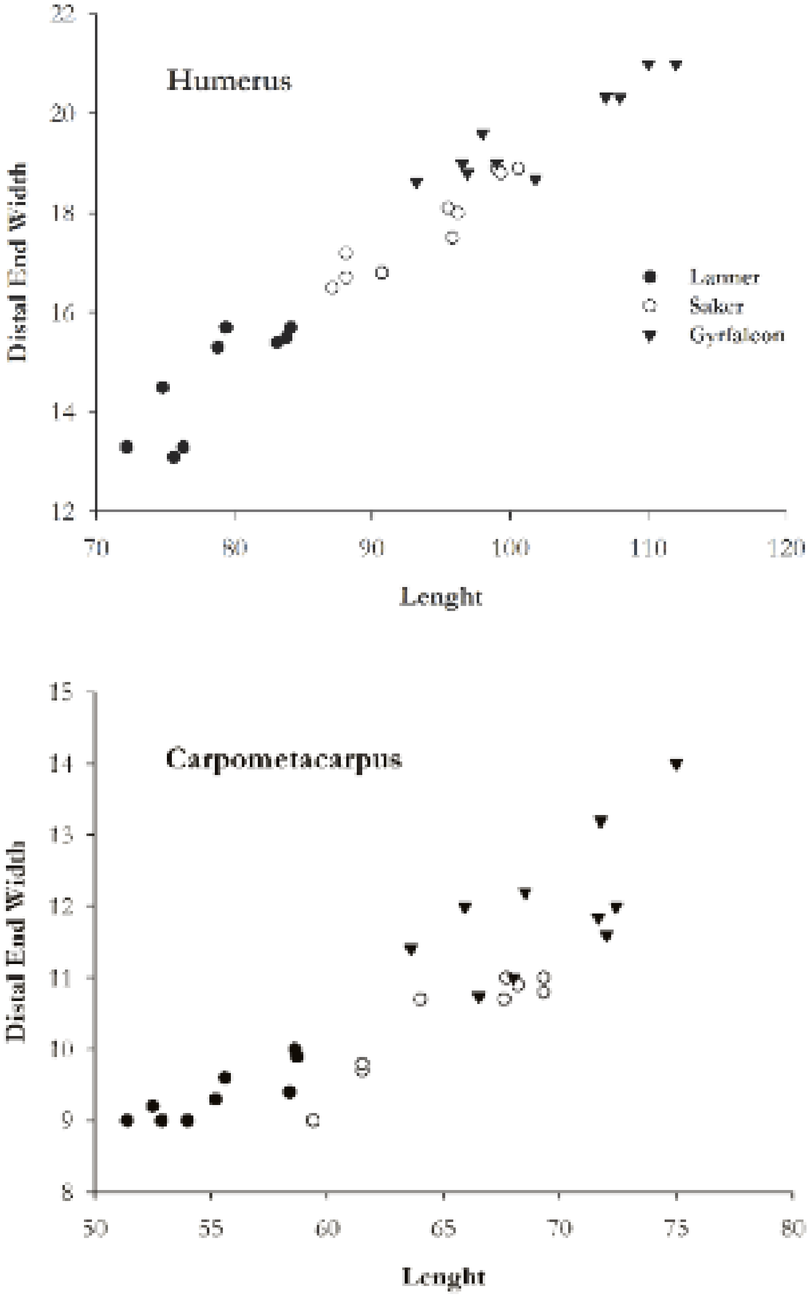


Figure 2.3 Comparative scatterplots of humerus and carpometacarpus measurements among three Hierofalcons (Lanner, Saker and Gyrfalcon) (Solti 1980, Solti 1981a, b, Louchart 2002, McNall M.C.E. Royal British Columbia Museum *www.royalbcmuseum.bc.ca/Natural_History/Bones/homepage.htm*).

FIGURE 2.4 Lanner falcon skull. Top (A) and bottom (B) views (length - 46 mm, width - 41 mm, height - 29 mm, bill length - 23 mm, total length - 69 mm). © and courtesy Wouter van Gestel (Experimental Zoology group, Wageningen University - *www.skullsite.com*).

and the Laggar falcon but different from Gyrfalcon and the Peregrine (Solti 1985). In particular, it is evident there is a clear difference in the humerus length between the Lanner falcon and the partially overlapping group composed of the Saker and the Gyrfalcon (Figure 2.3). A certain similarity occurs in measurements of the carpometacarpus bones due the large range found in the Saker, which spans the range found for the Lanner to the Gyrfalcon (Figure 2.3).

The ulnar of the Lanner falcon has a wide distal epiphyse and a large olecranon (Solti 1981b). Nevertheless, only measurements from the proximal epiphyse gave indexes (8.91-9.80) close to the Saker (9.59-9.90) due the above mentioned large olecranon (Solti 1981b, 1985). Jenkins (1995) reported a strong significant difference with the South African Peregrine (*F. p. minor*) where male Lanners have larger ulnar (90 mm) than their competitors (80 mm). This was not the same for females of these falcons where values were more similar (Jenkins 1995).

Among thorax bones, the length of the uncinate processes (that serve to attach scapula muscles) in extant birds does not vary phylogenetically but rather with the locomotor mode of the birds. The uncinate processes have a characteristic L-shaped morphology where they attach to the vertebral ribs and are uniform in thickness along the length of the process (average = 0.24 ± 0.01; Codd 2004). The length of the uncinate process of the Lanner falcon is 0.2142 (Codd 2004). Other measurements of the thorax include sternum length, width and depth (73.7-33.88-38.28 mm respectively) and the vertebral length (75.12 mm; Codd 2004).

2.2 Physiology

Data on the physiology, internal anatomy and histology of the Lanner falcon are very scarce in the published literature. Many findings are related to studies on pathogens or diseases, and mainly relate to captive birds. Although more general findings can be found in comprehensive studies regarding avian physiology, this refers to data strictly confined to the Lanner falcon.

Thermoregulation and water balance

The Lanner and the Laggar falcon appear to respond to increased ambient temperature sooner and more gradually than either Peregrine or Prairie falcon (Mosher and White 1978). Nevertheless, variations in body temperature do not necessarly correlate to climate in *Falconiformes* found in hot habitats (Wasser 1986). In common with other raptor species, the Lanner obtains most of its water from prey and seldom needs to drink, even when using evaporative cooling for several hours (Figure s3, Maclean 1996). Accordingly, the cloacal fluid is usually hypotonic to plasma (Cade and Greenwald 1966). Lanners therefore secrete fluid from a nasal gland to eliminate the excess of electrolytes (Cade and Greenwald 1966).

In the Kgalagadi Transfrontier Park (South Africa), 40.9°C is the ambient temperature at which the Lanner begins to display stress behaviour (ambient range temperature: min. 23.6 max. 45.1°C; Cordingley 2009). In order to avoid these high temperatures in Dhofar (Oman) in July, a Lanner falcon left his day roost site every evening at 16.00 (Walker 1981).

Metabolic rate

Field metabolic rates (FMR), individual mass and rate phenotypes are more directly ecologically relevant and are probably more directly subject to selection than resting rates and species-average phenotypes, respectively (Hudson *et al.* 2013). FMR has not been calculated directly for Lanners and, as very little data exists on FMR for *Falconiformes* in general, the general formula for all birds was used (Nagy 2005):

$FMR = 10.5\ M^{0.681}$

FIGURE S3 *F. b. biarmicus* drinking at a waterhole in the Kgalagadi Transfrontier Park, South Africa.© and courtesy of Maureen Gibson.

FIGURE S4 An adult *F. b. biarmicus* eating pebbles in South Africa. © and courtesy of Hugh Chittenden.

This formula can be used to calculate the daily energy demands of basal metabolism in kcal/day and applicable to falcons (Hudson *et al.* 2013). Overall, metabolic rate values are consistent with the heat dissipation theory of Speakman and Król (2010) and are negatively associated with annual temperature range an positively associated with and intra-annual coefficient of variation of precipitation (White *et al.* 2007). Thus, significant differences in FMRs are to be expected for Lanner falcon races adapted to a wide range of environmental types, ranging from arid to continental climates. Unfortunately, there are not enough weight data to allow for comparative calculations between races (see *Weights*). Nevertheless, a gross estimation of FMR using equation given by Nagy (2005) for adults *F. b. biarmicus* can be calculated as 758.14 kcal/day for males and 941.31 kcal/day for females (n = 8 females and 7 males; M. Parker and M. Wilson pers. data).

The blood system

At a microscopic level, blood of the Lanner falcon shows a heterophil, with a segmented nucleus and fusiform, brick-red cytoplasmic granules and an eosinophil with a bi-lobed nucleus and pale basophilic-grey cytoplasm with no distinct eosinophilic granules but with small pale "vacuoles" and finally typical small lymphocytes (Clark *et al.* 2009). Biochemical and cellular analysis from blood tests and other physiological parameters are listed in Table 2.5. It is possible to evaluate the cardiac size of the Lanner falcon as well as other large falcons through radiographic examinations (Barbon *et al.* 2010). Lateral and ventrodorsal radiographs from healthy Lanner falcons (9 females, 4 males) were examined to ascertain ratios with carina, chest (furcula and coracoid) bones (Barbon *et al.* 2010). Strong correlations exist between heart measurements and those of carina and chest but there is only a weak relationship with the coracoids (Barbon *et al.* 2010). Thus, regression equations need to be used in order to calculate both the length of the heart (4.2 + 0.53 × length of the sternum), and its width (7.13 + 0.54 × width of the chest or 21.58 + 3.08 × width of the coracoids; Barbon *et al.* 2010). In altricial and semi-altricial (ASA) birds, the embryonic heart rate (f_H) is maximal during the pipping (perinatal) period (Tazawa *et al.* 2001). Accordingly the f_H at 80% of the incubation duration for Lanner embryos was 242±9 (beats min^{-1}) and this increased rapidly two days prior to hatching (276±6; n = 2 *F. b. tanypterus* sp.; Tazawa *et al.* 2001). Also Lanner eggs followed the main allometric relationship for ASA birds where the maximum f_H was significantly related to measured fresh egg mass (41.2±0.4 g; n = 2; Tazawa *et al.* 2001).

The digestive tract

As pursuit predator, the Lanner falcon has a reletively small intestinal length around

General	Range
Respiration rate [a]	9.35 - 10.3
Heart frequency [b]	210 - 330
Body temperature [c]	41 - 42°
Complete blood count (CBC)	
Red Blood Cells (RBC)	2.63 - 3.98 × 10^2/l
White Blood Cells (WBC)	3.5 - 11 × 10^9/l
Packed cell volume (PCV)	0.37 - 0.53% l/l
Mean Corpuscolar Volume(MCV)	127 - 150^{fl}
Mean Corpuscolar Hemoglobin (MCH)	42.3 - 48.8 pg
Mean corpuscular hemoglobin concentration (MCHC)	317 - 353 g/l
Hemoglobin (Hb)	122 - 171 g/l
Albumin	9.6 - 16 g/l
Globulin	21.1 - 28.8 g/l
Albumin/Globulin ratio (A/G)	0.44 - 0.57
Serum chemistry	
Calcium	2.07 - 2.45 mmol/l
Glucose	11 - 15 mmol/l
Uric Acid	318 - 709 µmol/100ml
Urea	1.3 - 2.7 mmol/l
Creatinine	37 - 75 µmol/l
Cholesterol	3 - 8.8 mmol/l
Total protein	33 - 42 g/l
Alkaline phosphatase (ALP)	180 - 510 U/l
Phosphorus	0.68 - 2.0 mmol/l
Potassium	1 - 2.1 mmol/l
Sodium	152 - 164 mmol/l
Lactate dehydrogenase (LDH)	434 - 897 U/l
Aspartate aminotransferase (AST or SGOT)	30 - 118 U/l
Creatine Kinase (CK)	350 - 650 U/l

Table 2.5 Physiological values of the Lanner falcon, $n = 42$ for CBC e 26 for Serum analysis (Benyon 1996, Jennings 1996). (a) $n = 5$, (b) two males (450, 490 g), (c) cloacal temperature ($n = 1$ male; Mosher and White 1978).

800 mm, which is close to that of the Northern Goshawk (*Accipiter gentilis*) but still shorter than that of the Peregrine and Saker falcons (Hilton *et al.* 1999). These predators, whose hunting techniques requires rapid acceleration, would be under selection pressure to minimise the weight of all organ systems in the body in order to maximise the mass of the muscle systems involved in flight (Hilton *et al.* 1999). For this reason falcon species tend to have short, light digestive tracts, which also leads

to reduced weight of digested material due to the smaller gut volume and rapid excretion rate, as well as reduced intestine tissue mass (Hilton *et al.* 1999). A shorter gut lenght, however, results in reduced digestive efficiency and forces these predators to compensate by increasing their rate of prey capture (by at least and additional 7% of captures *per* day; Hilton *et al.* 1999). It is important that their prey includes species with high fat content (Hilton *et al.* 1999).

Several avian species improve their digestion by ingesting grit. This practice has been noted in a number of *Falconidae* species, including the Peregrine and other small falcon species as well as the Lanner (Thomsett 2007). Although ingestion of such material could well be accidental, the Lanner does seems to intentionally select and ingest grit with the probable intention of aiding digestion (Figure s4).

2.3 Melanins, carotenoids and the expression of plumage display

Eumelanin produces bold black patches as well black spots, bars, bands, and stripes which are found in the plumages of many avian species, whereas carotenoids are responsible for bright yellow, orange, and red plumage colours (Hill 2007). The former is synthesized by birds from amino acids and several metal ions (Ca, Zn, Cu, Fe) all of which are derived from their diet (Hill 2007). On the other hand, carotenoids are obtained by ingesting specific dietary carotenoid pigments as macromolecules and not from basic biological precursors (Hill 2007). Variations in expression of plumage display can be in the form of continuous variation both in hue, chroma, and brightness and/or extent of colour displays (Hill 2007). This variability remains as one of the main diagnostic criteria for the current classification of the Lanner falcon (Table 1.9; Neumann 1904). For example, the crown and nape ranged in colour from pale yellow (*F. b. erlangeri* sp.) to rufous

FIGURE 2.5 A young Lanner falcon (*biarmicus* sp, South Africa) showing melanin-based black patches and spots. The yellowish to rufous patterns of the head and nape from are carotenoid-based colourations (© and courtesy Malcolm Wilson).

Figure 2.6 An adult Lanner falcon (*F. b. biarmicus* sp.; North Central Kenya) showing lightly spotted breast, abdomen and flanks (© and courtesy of Darcy Ogada).

(*F. b. feldeggii* sp.) or intergrades from large spots and striped flanks (*F. b. feldeggii* and *F. b. tanypterus* sp.) to entirely unspotted abdomen (*F. b. biarmicus* sp.).

Thus, the Lanner falcon is considered a monomorphic but clearly polytypic species (Cramp and Simmons 1980, Roulin and Wink 2004). Taxonomic hypothese based on intergradation presumed the gradual (clinal) change of a character from one taxon to another ('*diagnosability*' criterion; Sangster 2014). In the case of the Lanner falcon group, of the taxa recognized and accepted taxa differ too much and should therefore be treated as separate subspecies ('*degree of difference*' criterion; Sangster 2014). Nevertheless, in the past, the clinal intergradation within populations has been traditionally treated as a criterion for differentiating subspecies (Table 1.9; many races not accepted). Although diagnostic phenotypic traits are apparent for *F. b. feldeggii* and *F. b. biarmicus* subspecies, no qualitative or quantitative analyses exist to support the current classification by the '*degree of difference*' criterion. Nevertheless, a preliminary study should be possible (see also the section on plumage patterns).

Eumelanic ornaments

Gloger's Rule states that, for a given species, more heavily pigmented individuals tend to be associated with more humid environments, with less-boldly coloured individuals found in drier climates (Roulin 2014). The frequency of light coloured individuals may therefore increase in the future, in regions where deserts are expanding, and that of darker coloured individuals increase in regions where humidity is predicted to increase (Roulin 2014). One of the reasons for this association is that melanin pigments have numerous pleiotropic effects that can improve individual fitness and provide a degree of resistance to environmental stress factors (Roulin 2014).

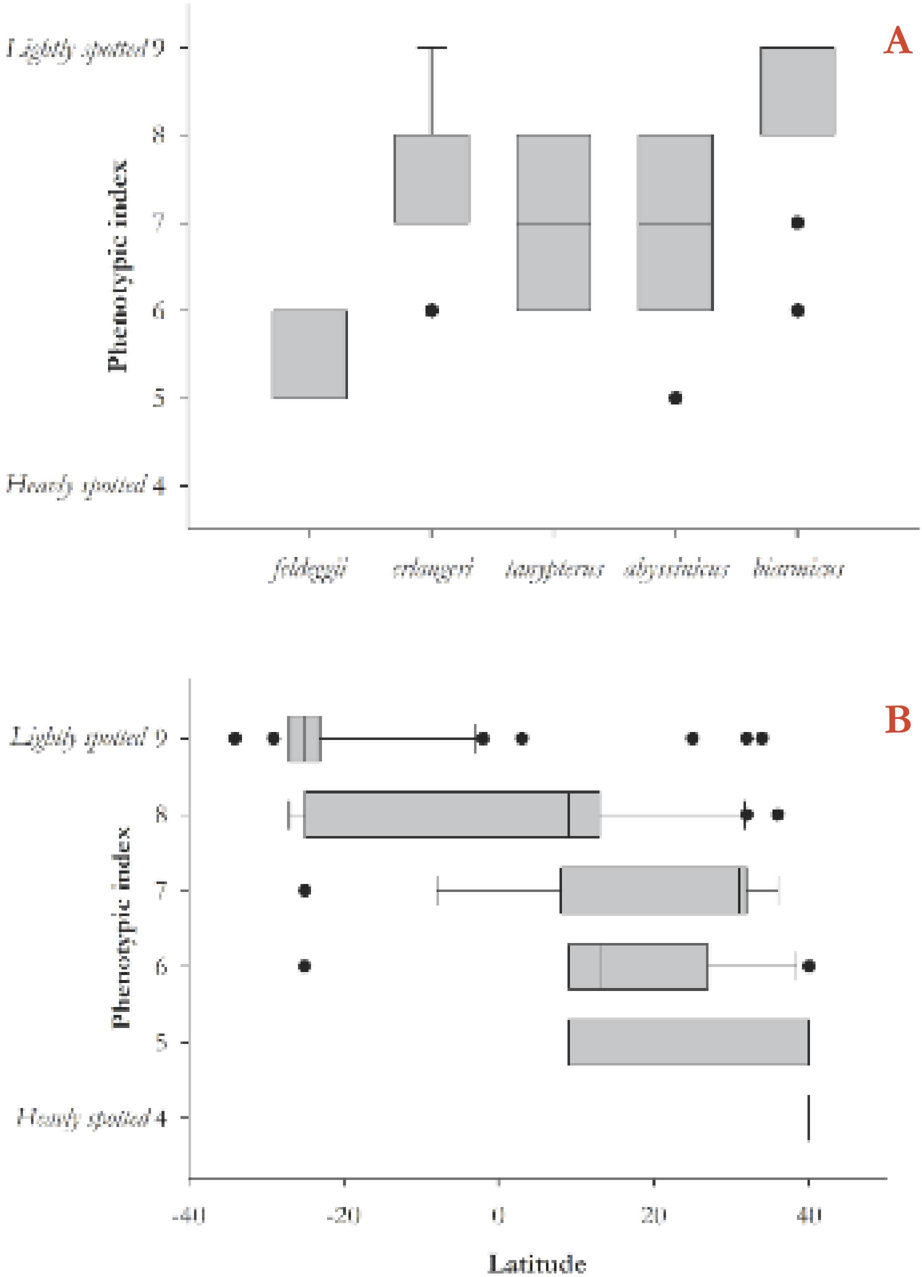


Figure 2.7 Subspecific (A) and clinal (B) variations in eumelanic ornaments of upper breast, breast and leg feathers expressed as phenotypic index (from heavily spotted to lightly spotted). For methodology details see '*Plumage patterns*' and Table 2.16 ; $n = 240$). The boundaries of the box indicate the 25th and the 75th percentile and a line within the box marks the median.

For example, in Peregrine and Barbary falcon populations, diagnostic phenotypic patterns were observed for moustache, cheeks and the distribution and density of spots (Zubergoitia *et al.* 2009, Rodríguez *et al.* 2011).

Eumelanic ornaments of upper breast, breast and leg feathers expressed as phenotypic index varied among Lanner falcon subspecies (Figure 2.7A). Published studies show that the *F. b. feldeggii* and *F. b. biarmicus* races represent the maximum limits of spotted and the unspotted respectively (Figure 2.7A). The variations shown by the other three subspecies were not significant except for a portion of pale to very pale individuals of the *F. b. erlangeri* race inhabiting desert areas of Morocco, Algeria and northern Mauritania (Figure s5). Similar patterns should be noted for *F. b. tanypterus* of the south-western desert in Egypt (Figure 2.8; Goodman and Haynes 1989). Nevertheless, hyper-dry climates drive colour intensity as well of eumelanic spots but individuals not become unspotted (Figure s5; see also *Plumage patterns*). In fact, this pattern is heritable and only weakly condition dependent (Roulin *et al.* 2008). For instance, majority of adult *F. b. biarmicus* individuals showed lightly spotted to completely underparts (Figures 2.6, s6).

The relative density of spots and stripes shows a clear subdivision between lower and higher latitudes in relation to the equator (Figure 2.7B). It seems that this melanin-based trait of the Lanner falcon is in accordance with Gloger's rule and may

Figure 2.8 A pale Lanner falcon (*F. b. tanypterus*) observed in the hyper-arid south-western desert in Egypt (© and courtesy C. Vance Haynes).

Figure s5 A very pale *F. b. erlangeri* individual, perched on a rock outcrop at Tamanrasset province in Algeria. © and courtesy of Redouane Tahri.

Figure s6 Perched adult *F. b. biarmicus* showing a typically unspotted abdomen and flanks (Kgalagadi Transfrontier Park, South Africa). © and courtesy of Brett E. Ellis.

well have a positive thermoregulatory effect in reducing resting basal metabolic rates at lower temperatures (Zink and Remsen 1986). In fact, dark surfaces absorb and radiate heat more rapidly than pale surfaces, meaning that in cooler climates birds can warm up more rapidly (Margalida *et al.* 2008). Nevertheless, it is expected that it is mainly temperature (correlated with the distance to the equator) and precipitation that have the strongest effects on the expression of this pattern, as well as other plumage traits (see *Plumage patterns*).

Several falcon species have two round or elliptical ocelli in the back of their head, generally of a lighter colour than the surrounding feathers (Negro *et al.* 2007). Conversely, the Lanner falcon nape shows dark patches surrounded by a lighter colour and a triangular dark stripe pointing down that separates the two spots, which may mimic a raptor's bill (Figure s7; Negro *et al.* 2007). This plumage pattern, along with the short neck of the Lanner falcon, combine to create an image that resembles the face of an owl (Negro *et al.* 2007). Predators with false faces such as this mainly feed upon small birds and live in open habitats. This conspicuous visual signal could be used to deceive mobbing birds so they can be more easily preyed upon (Negro *et al.* 2007). Finally, the malar stripes of falcons, located frontally, are potential aposematic visual signals warning of aggressive defensive behaviour that could be a warning to larger predators (Figure s8; Newman *et al.* 2005).

Carotenoids

As mentioned above, primitive plumage colouration mechanisms of falcons is based on the presence/absence of melanin pigmentation but the carotenoids required for more elaborate colouration mechanisms must be acquired from food (Hill 2007). Carotenoids are also important for health as they are precursors of vitamin A and also have a role to play as immuno-stimulants (Hill 2007). Among raptors, the concentrations of vitamin A in blood plasma is species-specific (and also varies between wild and captive states) due to different nutritional strategies (Schink *et al.* 2008, Müller *et al.* 2012). Similarly, vitamin E protects lipids from peroxidation and in combination with vitamin C has a more beneficial antioxidant effect (Marri and Richner 2014). Nevertheless, the sensitivity of birds to carotenoid deprivation appears to vary substantially among species (Karu *et al.* 2008, Schlegel 2013). In fact, carotenoid-based colouration can be correlated with significantly increased growth rate of nestlings when the chicks received supplemental vitamins (Marri and Richner 2014).

One captive Lanner falcon of the nominate race, found dead in a poor condition of health, was found to show a very low concentration of vitamin E in the liver (0.90 mg/kg wet wt.; Schlegel 2013). This bird had apparently been fed almost exclusively on frozen and thawed adult mice, a diet known to lead to vitamin E depri-

FIGURE S7 Back view of the head of an adult *F. b. biarmicus* in Limpopo province, South Africa. © and courtesy of Malcolm Wilson.

FIGURE S8 Lateral view of the head of an adult *F. b. biarmicus* in Limpopo province, South Africa. © and courtesy of Malcolm Wilson.

vation (Schlegel 2013). Supplementing diet with vitamins E and C has been shown to improve plasma levels as well as individual reproductive success (Dierenfeld *et al.* 1989, Marri and Richner 2014). Another individual also fed with mice also showed, as with the dead bird mentioned above, low levels of vitamin E in blood serum (3.5 mg/L - normal range 16.7-46.1 mg/L) but with a value of vitamin A (1.7 mg/L) analogous to other two Lanner falcons (1.34 to 2.11 mg/L; Schlegel 2013). After these findings, the bird was fed a vitamin-enriched mouse daily for nine months that provided 547 IU vitamin E/kg, 201 mg thiamin/kg, 13 mg lutein/kg, and 579 μg zeaxanthin/kg (Schlegel 2013). Levels of serum vitamin E and the coloration of bare parts, such as bill and legs, improved greatly but still did not reach normal conditions (Schlegel 2013). These findings suggest the importance of diet variability and feeding choice for maintaining vitamins levels, as well as the importance of avian prey as sources of carotenoids that enhance appropriate coloration (Schlegel 2013).

2.4 Morphology

Morphology refers to the description and comparison of forms, used mainly for an understanding of avian classification. In the past, body size and other structural features (mainly wing length) were used to recognize subspecies of the Lanner falcon (Table 1.9). Nevertheless, although wing length is a generally reliable indicator of body size, it is not an infallible and alternative measures have been recommended for the purposes of differentiating subspecies (for example weight; Zink and Remsen 1986). Reliance on morphological measurements is further complicated by the limited number of available published measurements of Lanner falcons, and in several parts of the distributional range such measurements are very scarce (especially for the *F. b. abyssinicus*). In addition, measurements from museum skins and those from wild birds are not always directly comparable due to differences between naturalized and live birds. This lack of data does not therefore allow for easy comparisons among races. Among subspecies, the most complete data sets available are for the nominate race of Southern Africa (Table 2.23; Biggs *et al.* 1979, Mendelsohn *et al.* 1989, Jenkins 1995).

Tail/wing ratio

The most frequent measures available in the published literature are forewing and tail lengths (see Tables 2.6-2.15). Figure 2.9 shows the differences in tail/wing ratio between Lanner falcon subspecies based on the available published data. Amadon (1943) suggested that tail/wing ratios is directly related to longer wings that, in turn, greatly improve the flight performances of migratory birds. In fact when migratory distances increase, morphological shift become evident which results in a larger forward component in flight due to a more prominent distal part of the wing (Norberg 1990). As a consequence of this adaptation, the more slender and pointed wings, along with the shorter tail length relative to the wing length, reduce the induced drag of the wings and produce greater uplift and thrust (Norberg 1990). The data suggest that the *F. b. erlangeri* race seems to have developed a '*migratory type*' flight apparatus with a more efficient morphology than their less migratory conspecifics (Figure 2.9). Movements of this race include long distance flight along pathways from Morocco to Mauritania (Banc d'Arguin) and occasionally to Senegal (Curry-Lindahl 1981; see Chapter 8). Nevertheless, this tendency not true for the whole of the north-western population and so the species as a whole is not considered truly migratory species (Curry-Lindahl 1981). In fact, Ledant *et al.* (1981) assumed that some migrant birds of the *F. b. erlangeri* sp. seldom reach as far as the Sahara resident populations found in the southern desert areas of Algeria.

It is, however, debatable whether pairs of birds in desert areas can be truly considered as '*residents*' (see 6.6). According to Jany (1960), pairs that exclusively exploit migrating small birds for rearing young need to move to their breeding areas every

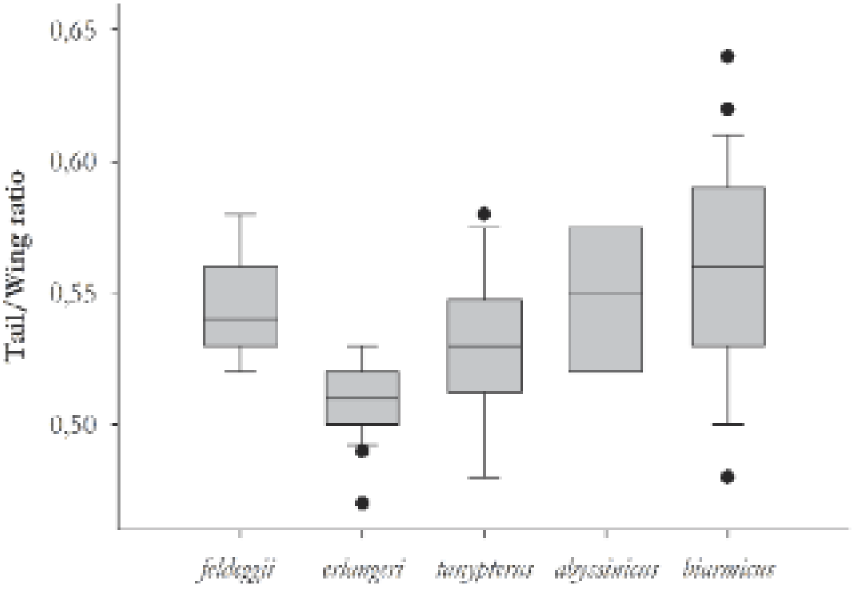


Figure 2.9 Tail/wing ratios among Lanner falcon subspecies. Male and female measurements are pooled (Blanford 1870, Kleinschmidt 1901, Martorelli 1911, Friedman 1930, Cramp and Simmons 1980, Goodmam and Abdel Mowla Atta 1987, Yosef 1988, Massa *et al.* 1991, Chiavetta 1992, Stephenson 2001, M Parker and M Wilson pers. data).

year and then leave these areas outside the breeding season due to the absence of alternative prey out the seasonal migration periods. Such behaviour is apparent in hyper-arid zones of plain desert such as in Mauritania, Chad, Algeria and the Western desert (see 6.6 and Chapter 7). In semi-arid environments of the Maghreb, Egypt and the Middle East, alternative prey species are available year round (i.e. mammals, invertebrates; see Chapter 7). Clearly, subspecies such as *F. b. erlangeri* and *F. b. tanypterus* which are associated with large uneven terrains such as deserts show an adapted flight apparatus (Figure 2.9). As with other genera such as *Oenanthe*, *Sylvia* and *Emebriza*, intraspecific differences in wing/tail ratio are expected for races that travel longer distances due to the adaptive need for more effective use of energy-efficient flight (Figure 2.9). Interestingly, in the case of the Lanner falcon the nominate race the available data show a wide range of ratios (Figure 2.9). This may be due to the fact that in arid regions where large scale fluctuations in prey density may occur, Lanner falcons (both adults and *juveniles*) may have a need to disperse long distances from their breeding sites outside the breeding season (max. 2087 Km; Little 1991, Herremans and Herremans-Tonnoeyer 1996).

Total length

Body length and wing length are characteristics that provide a fairly good estimate of overall body size (Wiklund 1996). Body size influences many aspects of an individual's biology such as behaviour, ecology and physiology (Wiklund 1996). Values for the measurement of the wing chord are common in the published literature, but not for body length (Ashton 2002). In fact, only broad measurements are available in the literature for all races with the notable exception of Jenkins (1995) who provides detailed ranges for males (39.0 ± 1.1; $n = 19$) and females (44.4 ± 1.6; $n = 16$) of the nominate *F. b. biarmicus* sp. Clark (1999) reported a range of 38-49 cm (mean 44) for Palearctic races (*F. b. feldeggii*, *F. b. erlangeri* and *F. b. tanypterus*) but Corso (2000) estimated 40-53 cm only for *F. b. feldeggii*.

Bergman's Rule states that birds in colder climates have larger bodies (Ashton 2002). This rule seems to hold true for bird species, and it appears that there is a significant positive overall relationship between body size and latitude and a significant negative relationship of size and temperature (Ashton 2002). A general comparison among subspecies also revealed a different trend for body length between sexes (Figure 2.10; see *Differences among sexes*). Ashton's review (2002) suggested that Bergmann's rule is stronger for sedentary than migratory species, and stronger for males than females, and that it applied more strongly to temperate than tropical taxa. In line with these generalisations, it appears that tropical subspecies of the Lanner falcon (*F. b. biarmicus* and *F. b. abyssinicus*) do not follow Bergmann's rule with respect to latitude (Figure 2.10). The Palearctic races showed a negative effect on

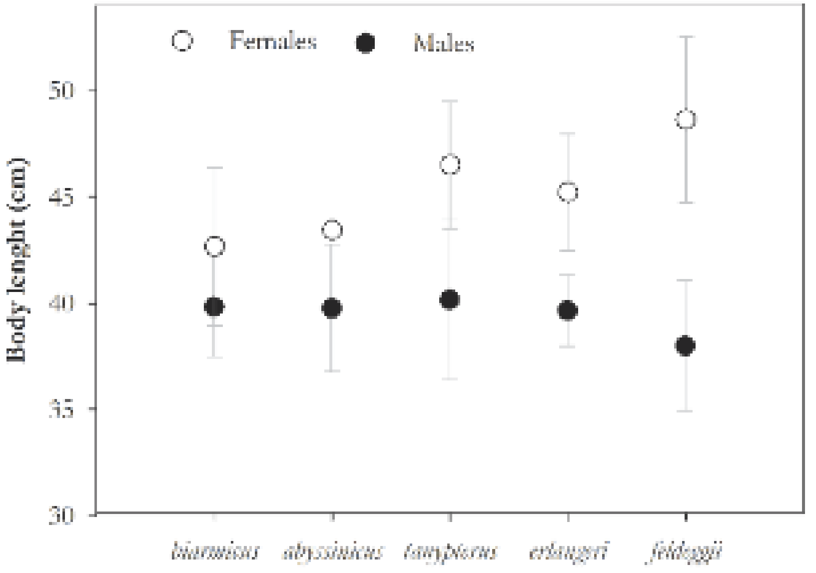


Figure 2.10 Male and female body lengths of Lanner falcon subspecies (Cuvier *et al.* 1827, Cavendish Taylor 1859, Shelley 1871, Dresser 1871-1881, Irby 1895, Layard and Sharpe 1897, Erlanger 1898, Stark and Scater 1900, Whitaker 1905, Langford 1912, Grant and Lowe 1915, Paris 1921, Cramp and Simmons 1980, Mirabelli 1982, MacLean 1984, Chiavetta 1992, Jenkins 1995, Clark 1999, Forsman 1999, Corso 2000).

on total body length in males and conversely an increase in females (especially for *F. b. feldeggii*; Figure 2.10). The consequences of this can be observed in the increased of dimorphism between males and females of the Palearctic races (Figure 2.10).

Wing and tail measurements

These are the most frequent morphological traits measured in published studies (Wiklund 1996, Ashton 2002). Tables 2.6 to 2.15 summarize the main data from published sources and regarding all subspecies. Unfortunately, the data are deficient for several races especially *F. b. abyssinicus* (Tables 2.9 and 2.14). In addition, many of these measurements are derived almost exclusively from museum specimens, as well as from historical sources, and very few of the published values are derived from field studies. However, there are good data sets of measurements, as well as other morphological and biological aspects, collected in the field for *F. b. feldeggii* and *F. b. biarmicus* (mainly *F. b. biarmicus*; Tables 2.10 and 2.15).

A comparative analysis of these different samples is necessary to avoid any bias due to the accuracy of measurements. Overall, results of one-way ANOVAs do not

Mean	Sex	Age	n	SD	Range	Reference
316.9	M	ad	7	6.10	310 - 330	Massa *et al.* 1991
315.9	M	ad	9	8.05	300 - 329	Chiavetta 1992
316.5	M	ad	2	9.19	310 - 323	Cramp and Simmons 1980
321.7	M	ad	13	14.6	307 - 344	Martorelli 1911, Hartert 1915, Paris 1921, Orlando 1957
317.0	M	juv	8	6.45	308 - 327	Cramp and Simmons 1980
323.2	M	juv	5	23.7	292 - 347	Martorelli 1911
346.5	F	ad	18	8.20	325 - 355	Massa *et al.* 1991
351.6	F	ad	10	9.89	335 - 371	Chiavetta 1992
347.0	F	ad	8	10.5	326 - 359	Cramp and Simmons 1980
355.4	F	ad	15	9.99	340 - 374	Hartert 1915
351.0	F	juv	21	4.67	340 - 360	Cramp and Simmons 1980
357.6	F	juv	7	17.6	321 - 375	Martorelli 1911

Table 2.6 Wing measurements of *F. b. feldeggii*. M = male, F = female, ad = adult, juv = *juveniles*. There are no significant differences between the samples (males $F = 0.584$, $p = 0.631$; females $F = 2.816$, $p = 0.049$; a slight but not significant difference with Hartert (1915) data - Bonferroni t-test $p = 0.058$) or between adults and young birds (males $F = 0.441$, $p = 0.817$; females $F = 2.456$, $p = 0.041$). Again, a slight but not significant difference with Martorelli (1911) and Hartert (1915) data (Bonferroni t-test $p = 0.151$). Massa *et al.* (1991) found similar trends from historical data, with any slight differences due to presumed measurement inaccuracies.

Mean	Sex	Age	n	SD	Range	Reference
324.0	M	ad	20	8.85	308 – 342	Cramp and Simmons 1980
320.5	M	ad	16	13.9	300 – 352	Martorelli 1911, Meinertzhagen 1920, Hartert 1912, Brown *et al.* 1982, Yosef 1988
298.0	M	juv	2	4.24	295 – 301	Dresser 1871-1881, Martorelli 1911
365.0	F	ad	8	4.75	356 – 370	Cramp and Simmons 1980
360.8	F	ad	13	14.4	333 – 375	Dresser 1871-1881, Neumann 1904, Hartert 1912, Brown *et al.* 1982, Goodmam and Abdel Mowla Atta 1987
355.0	F	juv	1			Martorelli 1911

Table 2.7 Wing measurements of *F. b. tanypterus*. M = male, F = female, ad = adult, juv = *juveniles*. No significant differences among samples (males $F = 0.844$, $p = 0.365$; females $F = 0.627$, $p = 0.438$). Insufficient data for comparisons between adult and young birds. Possible measurement inaccuracies.

Mean	Sex	Age	n	SD	Range	Reference
308.4	M	ad	7	12.0	295 – 327	Massa *et al.* 1991
313.0	M	ad	5	6.44	305 – 322	Cramp and Simmons 1980
314.7	M	ad	21		308 – 324	Hartert 1912
313.2	M	ad	5	9.21	308 – 330	Erlanger 1898
312.3	M	ad	6	0.74	303 - 324	Kleinschmidt 1901
311.1	M	ad	9	7.83	300 - 324	Whitaker 1905, Martorelli 1911, Simon 1965, Brown *et al.* 1982
295.0	M	juv	2	21.21	280 – 310	Erlanger 1898
341.2	F	ad	11	16.1	313 – 365	Massa *et al.* 1991
343.0	F	ad	5	5.10	338 – 349	Cramp and Simmons 1980
350.0	F	ad	14		338 – 359	Hartert 1912
347.0	F	ad	5	7.28	339 – 356	Erlanger 1898
347.6	F	ad	5	0.59	341 - 355	Kleinschmidt 1901
349.6	F	ad	9	9.72	338 – 359	Whitaker 1905, Brown *et al.* 1982
338.0	F	juv	1			Martorelli 1911

TABLE 2.8 Wing measurements of *F. b. erlangeri*. M = male, F = female, ad = adult, juv = *juveniles*. No significant differences among samples (males $F = 0.359$, $p = 0.783$; females $F = 0.921$, $p = 0.445$). Insufficient data for comparisons between adult and young birds. Possible measurement inaccuracies, especially from Erlanger (1898). Data from Kleinschmidt (1901) include those collected by Erlanger (1898).

reveal significant difference among samples when comparing adult and *juvenile* birds (see captions on Tables 2.6-2.15) according to Jenkins (1995) and Stephenson (2001). Nevertheless, some *juveniles* appeared to have longer flight feathers and lighter wing loadings that probably increase their survival chances through increased manoeuvrability and reduced energetic costs of flight (Jenkins 1995). Further analyses such as tail/wing ratios (see page 64), Reversed Size Dimorphism (see page 93) and Unrooted NJ morphological trees (see Figure 2.26) are also based on this comprehensive dataset. In common with species such as Gyr- and Saker falcons, the Lanner falcon tends to have more rounded wings with shorter outermost primaries. When perched, its wing-tips normally fall well short of its tail-tip (Corso 2000).

Few data exist on wingspan measurements. Pooled males and females *F. b. tanypterus* 90-109 cm, *F. b. feldeggii* 89-125 cm, Palearctic races 90-115 (Cramp and Simmons 1980, Clark quoted in Forsman 1999, Corso 2000). Males *F. b. feldeggii* 87-95 cm and females 95-105 cm (Mirabelli 1982). Young *F. b. biarmicus* males 94 cm (SD= 3.2 cm), male adults 94.2 (SD=1.25 cm) and females 110.5 cm (Mundy and Hartley 2002).

Mean	Sex	Age	n	SD	Range	Reference
332.1	M	ad	12	11.87	310 – 346	Blanford 1870, Neumann 1904, Hartert 1912, Grant and Lowe 1915, Friedman 1930, Brown *et al.* 1982
372.6	F	ad	18	13.1	343 – 390	Blanford 1870, Neumann 1904, Martorelli 1911, Hartert 1912, Friedman 1930, Brown *et al.* 1982
398.0	F	juv	1			Friedman 1930

TABLE 2.9 Wing measurements of *F. b. abyssinicus*. M = male, F = female, ad = adult, juv = *juveniles*. Insufficient data for comparisons among adult and young birds.

Mean	Sex	Age	n	SD	Range	Reference
305.7	M	ad	15	9.91		Mendelsohn *et al.* 1989
313.0	M	ad	4	3.90	308 – 317	Stephenson 2001
318.0	M	ad	2			M. Wilson and M. Parker unpubl. data
309.4	M	ad	14	11.2	292 - 317	Layard and Sharpe 1897, Stark and Sclater 1900, Brown *et al.* 1982, Dowsett 2009
315.0	M	*	19	11.0		Jenkins 1995
308.5	M	ad	4	16.8	285 – 323	Mundy and Hartley 2002
317.0	M	ad	9		308 – 332	MacLean 1984
317.0	M	juv	3	1.50	316 – 319	Stephenson 2001
317.0	M	juv	11	11.9	305 – 342	M. Wilson and M. Parker unpubl. data
320.7	M	juv	4	14.1	308 – 340	Mundy and Hartley 2002
341.1	F	ad	12	16.8		Mendelsohn *et al.* 1989
346.0	F	ad	11	13.5	326 – 361	Stephenson 2001
349.0	F	ad	3	3.05	346 – 352	M. Wilson and M. Parker unpubl. data
351.0	F	ad	13	12.2	330 – 372	Layard and Sharpe 1897, Stark and Sclater 1900, Martorelli 1911, Brown *et al.* 1982, Mundy and Hartley 2002
345.0	F	*	21	7.0		Jenkins 1995
350.0	F	ad	7		340 – 360	MacLean 1984
344.0	F	juv	9	15.8	314 – 360	Stephenson 2001
349.0	F	juv	4	11.6	338 – 362	M. Wilson and M. Parker unpubl. data
350.0	F	juv	1			Martorelli 1911
350.5	F	juv	2	7.78	345 – 356	Mundy and Hartley 2002

FIGURE 2.11 Dorsal view of an adult male *F. b. abyssinicus* captured in Burkina Faso. © and courtesy of Marco Pavia.

TABLE 2.10 Wing measurements of *F. b. biarmicus*. M = male, F = female, ad = adult, juv = *juveniles*. No significant differences among samples (males $F = 2.359$, $p = 0.083$; females $F = 1.120$, $p = 0.357$; and among adults and young birds (males $F = 2.193$, $p = 0.067$; females $F = 0.759$, $p = 0.604$). * = adults and *juveniles* pooled.

Mean	Sex	Age	n	SD	Range	Reference
167.5	M	ad	6	3.50	162 - 172	Massa *et al.* 1991
170.1	M	ad	7	10.86	157 - 186	Chiavetta 1992
169.0	M	ad	2	1.41	168 - 170	Cramp and Simmons 1980
170.0	M	juv	8	5.85	163 - 170	Cramp and Simmons 1980
180.7	M	juv	5	10.85	175 - 195	Martorelli 1911
185.6	F	ad	13	7.50	173 - 196	Massa *et al.* 1991
204.4	F	ad	10	5.89	195 - 214	Chiavetta 1992
193.0	F	ad	9	8.50	175 - 202	Cramp and Simmons 1980
194.0	F	juv	21	5.67	184 - 202	Cramp and Simmons 1980
208.7	F	juv	6	11.66	200 - 224	Martorelli 1911

Table 2.11 Tail measurements of *F. b. feldeggii*. M = male, F = female, ad = adult, juv = *juveniles*. There are variable significant differences among samples (males $F = 0.170$, $p = 0.846$; females $F = 18.542$, $p = <0.001$) and between adults and young birds (males $F = 2.184$, $p = 0.103$; females $F = 15.013$, $p =<0.001$). All pairwise multiple comparison procedures (Holm-Sidak method) between female samples gave high significant p values.

Mean	Sex	Age	n	SD	Range	Reference
154.4	M	ad	7	8.8	140 – 165	Massa *et al.* 1991
161.0	M	ad	5	4.16	156 – 166	Cramp and Simmons 1980
	M	ad	12		165 – 172	Hartert 1912
181.2	M	ad	5	5.21	176 – 190	Erlanger 1898
158.7	M	ad	6	0.35	154 - 163	Kleinschmidt 1901
165.0	M	ad	1			Simon 1965
160.0	M	juv	1			Erlanger 1898
176.5	F	ad	11	9.80	158 – 188	Massa *et al.* 1991
180.0	F	ad	6	5.30	172 – 187	Cramp and Simmons 1980
	F	ad	14		170 – 185	Hartert 1912
195.0	F	ad	4	13.54	175 – 205	Erlanger 1898
180.4	F	ad	5	0.58	171 – 186	Kleinschmidt 1901
190.0	F	ad	1			Martorelli 1911
190.0	F	juv	2			Erlanger 1898, Martorelli 1911

Table 2.12 Tail measurements of *F. b. erlangeri*. M = male, F = female, ad = adult, juv = *juveniles*. No significant differences among samples (males $F = 1.918$, $p = 0.181$; females $F = 0.646$, $p = 0.535$).Insufficient data for comparisons between adult and young birds. Data from Erlanger (1898) was excluded from comparative analysis for both males and females due to possible bias in the accurancy of measurements. However, the data from Kleinschmidt (1901) used for subspecies recognition closely matches with recent studies.

Mean	Sex	Age	n	SD	Range	Reference
166.0	M	ad	21	7.76	149 – 182	Cramp and Simmons 1980
166.0	M	ad	16	15.65	150 – 194	Martorelli 1911, Hartert 1912, Yosef 1988
174.5	M	juv	2	2.12	173 – 176	Dresser 1871-1881, Martorelli 1911
195.0	F	ad	8	6.57	186 – 207	Cramp and Simmons 1980
193.4	F	ad	5	7.37	183 – 200	Dresser 1871-1881, Hartert 1912, Goodmam and Abdel Mowla Atta 1987
190.0	F	juv	1			Martorelli 1911

TABLE 2.13 Tail measurements of *F. b. tanypterus*. M = male, F = female, ad = adult, juv = *juveniles*. No significant differences among samples (males F =0.000, p = 1.000; females F = 0.167, p = 0.691). Insufficient data for comparisons between adult and young birds.

Mean	Sex	Age	n	SD	Range	Reference
190.5	M	ad	1			Blanford 1870,
214.7	F	ad	3	22.8	200 – 241	Blanford 1870, Martorelli 1911, Friedman 1930
225.0	F	juv	1			Friedman 1930

TABLE 2.14 Tail measurements of *F. b. abyssinicus*. M = male, F = female, ad = adult, juv = *juveniles*. Insufficient data for comparisons between adult and young birds.

FIGURE 2.12 Tail of adult male *F. b. abyssinicus*. The tail is composed of twelve feathers. Burkina Faso. © and courtesy Marco Pavia.

Mean	Sex	Age	n	SD	Range	Reference
181.0	M	ad	4	11.0	170 – 196	Stephenson 2001
157.0	M	ad	2	4.94	153 – 160	M. Wilson and M. Parker unpubl. data,
166.0	M	ad	6	9.84	155 – 178	Layard and Sharpe 1897, Stark and Sclater 1900, Langford 1912, Brown *et al.* 1982, Dowsett 2009
159.0	M	*	20	7.0		Jenkins 1995
	M	ad	9		160 – 178	MacLean 1984
157.7	M	ad	4	3.2	155 – 161	Mundy and Hartley 2002
187.0	M	juv	3	6.6	182 – 195	Stephenson 2001
182.0	M	juv	10	29.6	160 – 200	M. Wilson and M. Parker unpubl. data
173.0	M	juv	4	10.6	163 – 187	Mundy and Hartley 2002
202.0	F	ad	11	10.4	188 – 218	Stephenson 2001
184.0	F	ad	3	7.64	177 – 192	M. Wilson and M. Parker unpubl. data
189.4	F	ad	8	11.15	173 – 210	Layard and Sharpe 1897, Stark and Sclater 1900, Martorelli 1911, Brown *et al.* 1982, Mundy and Hartley 2002
189.0	F	*	21	9.0		Jenkins 1995
	F	ad	7		185 – 210	MacLean 1984
206.0	F	juv	9	12.2	183 – 215	Stephenson 2001
192.0	F	juv	4	7.23	185 – 202	M. Wilson and M. Parker unpubl. data
189.5	F	juv	2	7.78	184 – 195	Mundy and Hartley 2002
200.0	F	juv	1			Martorelli 1911

Table 2.15 Tail measurements of *F. b. biarmicus*. M = male, F = female, ad = adult, juv = *juveniles*. No significant differences among samples (males $F = 2.175$, $p = 0.135$; females F 0.402, $p = 0.673$) and between adults and young birds (females $F = 0.439$, $p = 0.727$). All pairwise multiple comparison procedures (Holm-Sidak method) revealed significant p values only with data from Stephenson (2001) that was not used in the final analysis. Nevertheless, comparisons between adult and young males varied greatly depending on which samples were used. Jenkins (1995) pooled adult and young individuals due to the absence of significant differences. In addition, all samples ranged from 153 mm to a maximum of 178 mm, very much less than 196 mm reported by Stephenson (2001).

Plumage patterns

A plethora of plumage descriptions concerning different races can be found in both historical (*F. b. biarmicus* - Gurney 1862, Layard and Sharpe 1897, Stark and Scater 1900, Sharpe 1904, *F. b. abyssinicus* - Salvadori 1884, Ogilvie-Grant and Reid 1901, *F. b. erlangeri* - Whitaker 1905, *F. b. tanypterus* - Cavendish Taylor 1859, Warthausen 1860, *F. b.feldeggii* - Martorelli 1911) and more recent sources (Glutz *et al.* 1971,

Cramp and Simmons 1980, Brown *et al.* 1982, Forsman 1999, Clark 1999, Corso 2000) literature. Nevertheless, from the detailed descriptions in these sources we can only extrapolate a few remarks:
• *F. b. feldeggii* is the darkest race
• *F. b. erlangeri* is the palest (especially in desert areas)
• contact zones between races showed a certain intergrading of plumage patters (i.e. *F. b. erlangeri*/*F. b. abyssinicus* in W Africa, *F. b. tanypterus*/*F. b. abyssinicus* in southern Sudan and *F. b. abyssinicus*/*F. b. biarmicus* in Kenya)
• there persists a certain clinal variation in '*spottiness*' (see Figure 2.7 A,B).
Unfortunately, a key question remains unresolved: which mechanisms led to this variability?. The main aim of historical authors was to discern some diagnostic traits that could be used to unambiguously discriminate between each race (see Table 1.9). However, more recent literature has focused mainly on methods for field identification as well as differentiating between races or co-genres in the hand (Forsman 1999, Clark 1999, Corso 2000). Thus, any possible difference has been attributed to the peculiar characteristics of each subspecies (see Plate I). Based on these premises, it would appear to be very difficult to build a comprehensive overview.

Jany (1960) emphasized the importance of climate features on the Lanner falcon

FIGURE 2.13 An adult male *F. b. abyssinicus* sp. captured in Burkina Faso. Plumage patterns show the smaller spots in the breast and leg feathers which are clearly different from that of individuals from Ethiopia (see Figure s2)(© and courtesy Marco Pavia).

populations in North Africa with the pigment-rich *F. b. tanypterus* that occupies more humid Upper Nile and Red Sea areas. In the same way, Martorelli (1911) noted that individuals belonging to *F. b. biarmicus* become gradually more unspotted ranging from the Palearctic towards the southern African forms (see Figure 2.7). The findings of both Authors follows Gloger's ecogeographical rule, whereby darker birds are predicted to be found in areas with greater humidity (precipitation), and lighter birds in more arid areas (Zink and Remsen 1986).

In line with other studies on plumage variations, a phenotypic index could be calculated based on scores for each diagnostic trait (Table 2.16; Zubergoitia *et al.* 2009, Rodríguez *et al.* 2011). As expected, several of the key plumage features drives total variance (Table 2.17). They include head (crown and nape), breast and leg feathers patterns (PCA1, Table 2.17).

Frequencies of phenotypic index values divided by subspecies revealed a closed relatedness among afrotropical (*F. b. biarmicus*/*F. b. abyssinicus*) and also North African (*F. b. erlangeri*/*F. b. tanypterus*) races with darker *F. b. feldeggii* clearly separated from

Feature	Scores		
	1	2	3
Head colour	Rufous	Pale	-
Superciliary	Clearly visible	Small	Absent
Eye-stripe	Uniform patch with the moustache	Fragmented but large patch	Less width patch
Crown	Clearly visible stripes	Less rufous stripes	Single uniform patch
Forehead	Large black patch	Small black patch	Absent or less striped
Nape	Rufous stripes and large patches	Less rufous stripes and patches	Without stripes and small patches
Upper breast	Fully marked	Partially marked	Unmarked
Breast	Large spots	Small spots	Unspotted
Leg feathers	Barred	Spotted	Unspotted

Table 2.16 Plumage patterns and coded scores used for nine coloration characteristics following the procedures outlined in Zubergoitia *et al.* (2009) and Rodríguez *et al.* (2011). Photos of specimens (belonging to all of the subspecies of Lanner falcon) were derived from scientific literature, web-sites, private unpublished collections and from museums ($n = 693$). After a careful revision process, 473 pictures were excluded from this study based on a number of criteria including photographs of young specimens, captive birds, multiple shots of the same individual, absence of location, low-quality resolution images, and any photographs where race identification was uncertain. A Principal Components Analysis (PCA) was performed with the Varimax-Kaiser rotation as an exploratory tool. No difference analysis between sexes was performed.

	PCA1	PCA2	PCA3
Head colour	-0.082220	**0.837772**	0.012249
Superciliary	0.025568	-0.010195	**0.869023**
Eye-stripe	-0.089794	0.462567	-0.549591
Crown	**0.817294**	0.188821	-0.036842
Forehead	0.057662	**0.787508**	-0.153457
Nape	**0.781206**	0.205058	0.153351
Upper breast	0.597941	-0.421033	-0.180438
Breast	**0.758222**	-0.351964	0.085429
Leg feathers	**0.747003**	-0.249150	-0.003817
Eingenvalue	3.018	1.845	1.046
Explained Variance (%)	33.5	20.5	11.6

Table 2.17 Importance of coloration variables in Lanner falcon subspecies, with respect to each varimax-rotated factor of the principal components analysis (PCA). Factor loadings values larger than 0.7 are indicated in bold (see Table 2.16 for details).

the others (Figure 2.15). In addition, where a large sample size is available, the figure also shows a certain discrete distribution of values among populations (cf. *F. b. biarmicus* and *F. b. abyssinicus*). Therefore, it is likely that independent extrinsic factors have a fundamental role to play in affecting the plumage patterns of subspecies. From a strictly latitudinal point of view, Afrotropical and Western Palearctic races are not clearly separated populations based on their plumage patterns (Figure 2.14). Thus, intergrades in colour and patterns are equally plausible as well as those observed for spots and stripes (Figure 2.7).

The geographical variation in the plumage of Lanner falcons is clearly evident in relation to local mean annual temperatures (Figure 2.16). This strong relationship is also apparent in the variability observed between races when they are linked with different environments (i.e. paler forms in hot zones and darker individuals in cool environments; Figure 2.16). Thus, thermoregulation may play more of a role in the plumage patterns associated with these populations (Walsberg 1983). Birds with darker plumages are better able to absorb the energy of solar radiation, and this may reduce their resting basal metabolic rates at lower temperatures (Hamilton and Heppner 1967). In addition, temperature may result in fitness differences between individuals which exhibit varying degrees of melanin coloration (Sirkiä *et al.* 2010). Such variations have been observed to affect the geographical distribution of colour types for several other avian and mammalian species (Sirkiä *et al.* 2010). In particular, the highest reproductive success of darker birds was when it was cold during egg-laying but warm during the nestling period (i.e. for the *F. b. feldeggii*), whereas the fledgling production of light-coloured individuals was highest when it was continuously warm

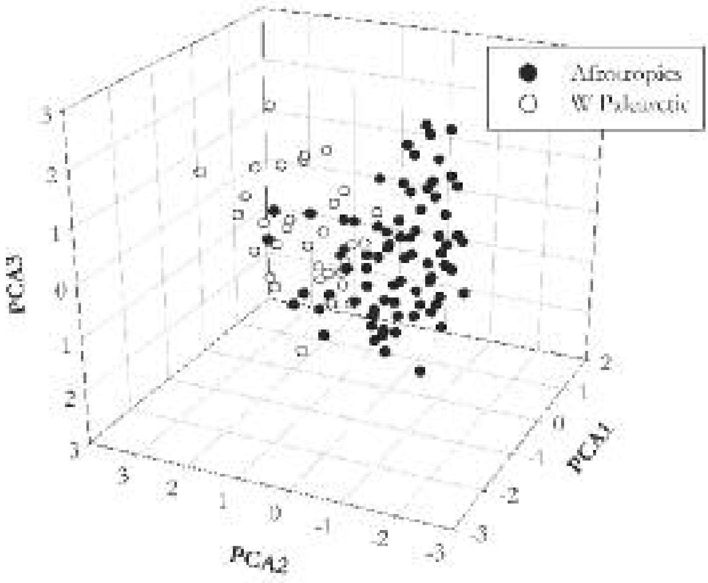


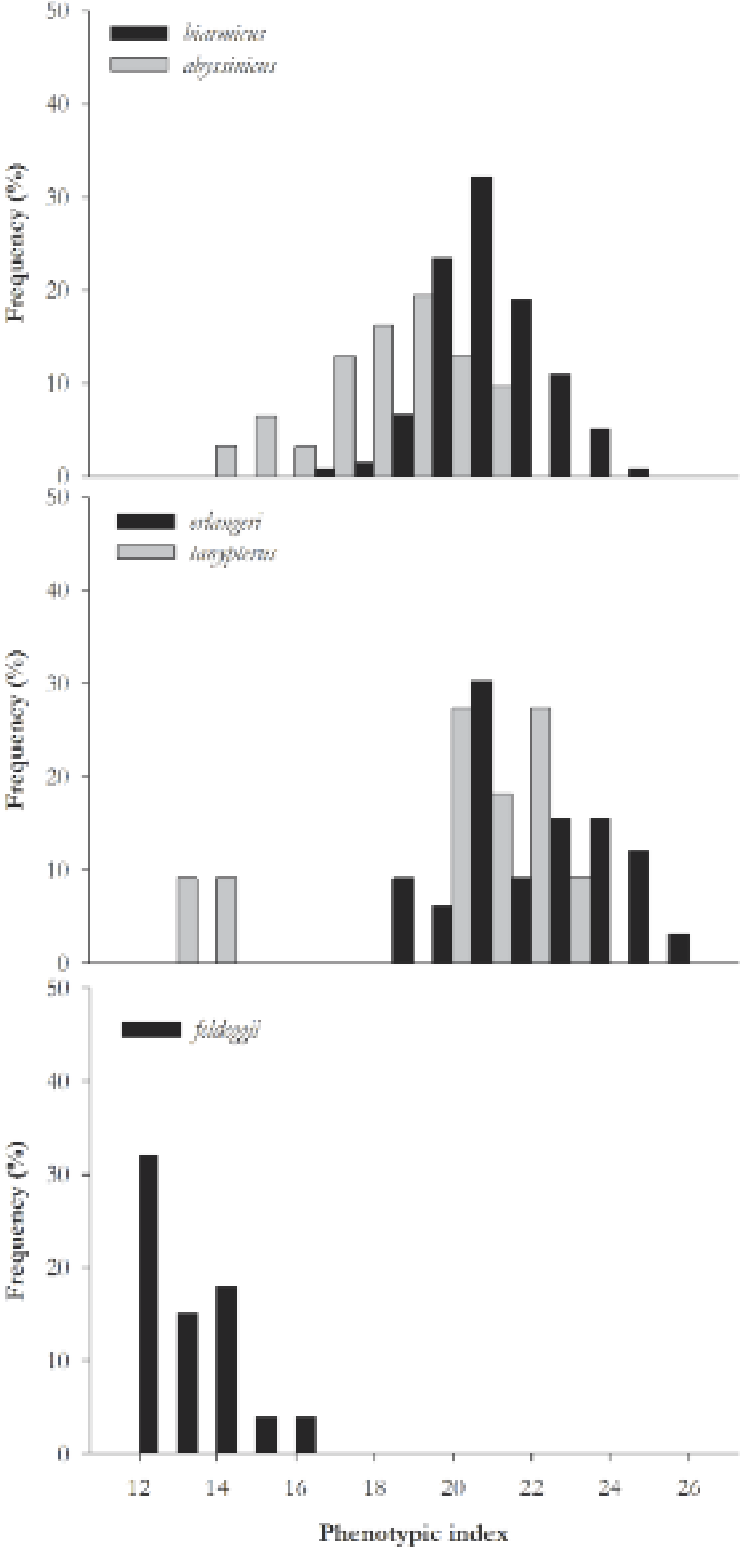
FIGURE 2.14 Ecozones (Afrotropics and Western Palearctic) associated with each specimen on the principal component axes.

(i.e. *F. b. biarmicus*; Sirkiä *et al.* 2010). In this way such morphological measurements and genetic differences, along with variations in plumage patterns, could help to understand the main factors that have led to the present distribution of the Lanner falcon (see 3.2).

Plumage care

Several pictures exist depicting adult and *juvenile* Lanner falcons taking water baths, especially in water holes of arid lands where they can also be found feeding on drinking prey (i.e. in Kgalagadi Transfrontier Park, South Africa). These dusting and bathing behaviours have also been observed in other African countries such as Ethiopia and Uganda. Most probably dust-bathing evolved from water bathing. Dusting removes excess feather lipids and should also have a positive effect on bird health by decreasing the number of ectoparasites present in the plumage. In common with other large falcons, the Lanner takes dust baths using both sitting and lying positions, which are also typical of water bathing (Schmidl 1985). An adult observed in Kwa-

FIGURE 2.15 Variation in the Lanner falcon subspecies phenotype index. Ranges span from darkest (12) to palest (26) values (see Table 2.16 for details; n = 240; *F. b. biarmicus* = 137; *F. b. abyssinicus* = 33, *F. b. tanypterus* = 21, *F. b. erlangeri* = 31, *F. b. feldeggii* = 18).


biarmicus
abyssinicus
erlangeri
tanypterus
feldeggii
Frequency (%)
Phenotypic index
0
10
20
30
40
50
12
14
16
18
20
22
24
26

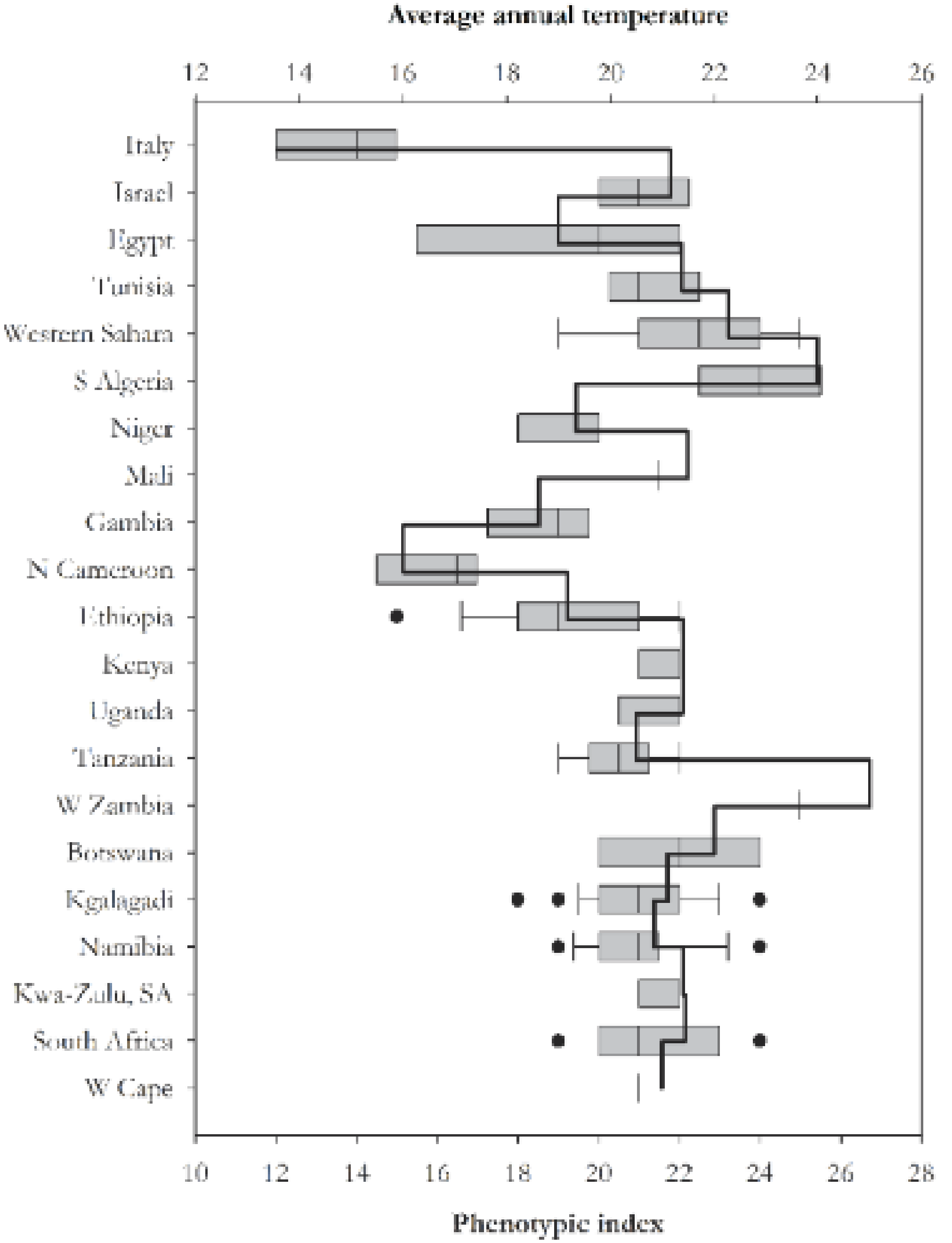


FIGURE 2.16 Variability of plumage phenotypic index (boxes) in relation to mean annual temperatures (lines) of several different localities of the distributional area of the Lanner falcon. Boundaries of the box indicate the 25th and the 75th percentile and a line within the box marks the median. Temperatures derived from the Climate Change Knowledge Portal (CCKP)(*http://sdwebx.worldbank.org/climateportal/index.cfm*).

Zulu-Natal stayed on its right side (lying position) in the sand with one leg ruffling dust through the plumage (Schmidl 1985).

Feathers

The rachis, made of β keratin, is the main structure of feathers and, along with the hierarchical structure and morphology of the feather filaments themselves, contributes to the extreme mechanical strength and flexibility of bird feathers (Lingham-Soliar *et al.* 2010). Using a scanning electron microscope (SEM), a fibre diameter of approximately 6 μm was found to be rather constant in the feathers of a number of bird species including the Lanner falcon (Figure 2.17). At a wider level (100 μm), barbs adjacent to the rachis of Hierofalcon feathers seems to have a structure that leads to the soft and flexible plumage characteristics when compared to that of, for instance, the Peregrine falcon (White 1996). This trait could well be related to the improved flight performance required by the hunting activities that these falcons (Lanner, Saker, and Black - falcons) adopt in open arid habitats (White 1996).

The length of primary feathers is also a diagnostic feature with P10 (12 - 20) usually equal or shorter than P8 and P9 being the longest (Cramp and Simmons 1980, White 1996). Measurements ranges for the primary feathers are P10 (12-20), P8 (4-12), P7 (20-32), P6 (43-55), P5 (63-83), P1 (145-159) for males and P1 (152-177) for females (Cramp and Simmons 1980).

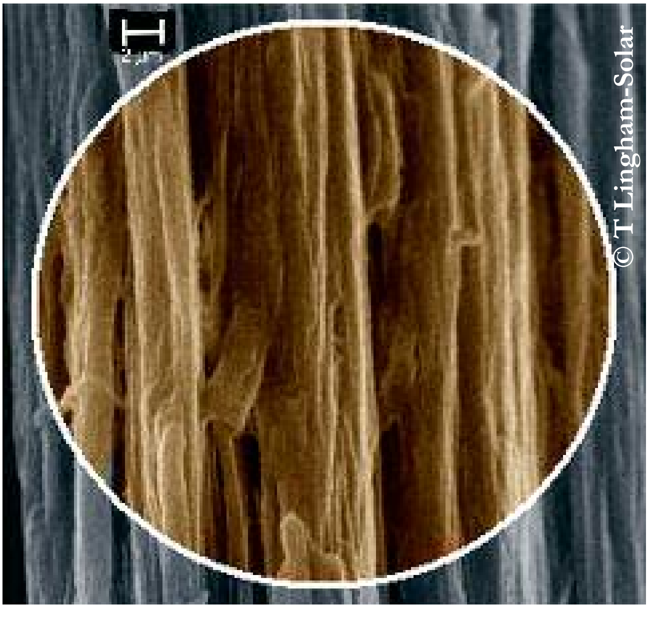


FIGURE 2.17 Fibres from a taxidermy specimen of *F. b. biarmicus* with the matrix degraded, and somewhat superficially degraded but intact fibres. (© and courtesy T. Lingham-Soliar).

Other characteristics of feathers which have been determined by previous Authors (*cf.* Hartert 1912) include the fact that the outer web of P8 and P9 and inner P9 are emarginated and the inner web of P10 is notched (Cramp and Simmons 1980).

The tail is composed of twelve feathers with T6 (ca. 18 mm) shorter than T1 (Figure 2.12; Cramp and Simmons 1980).

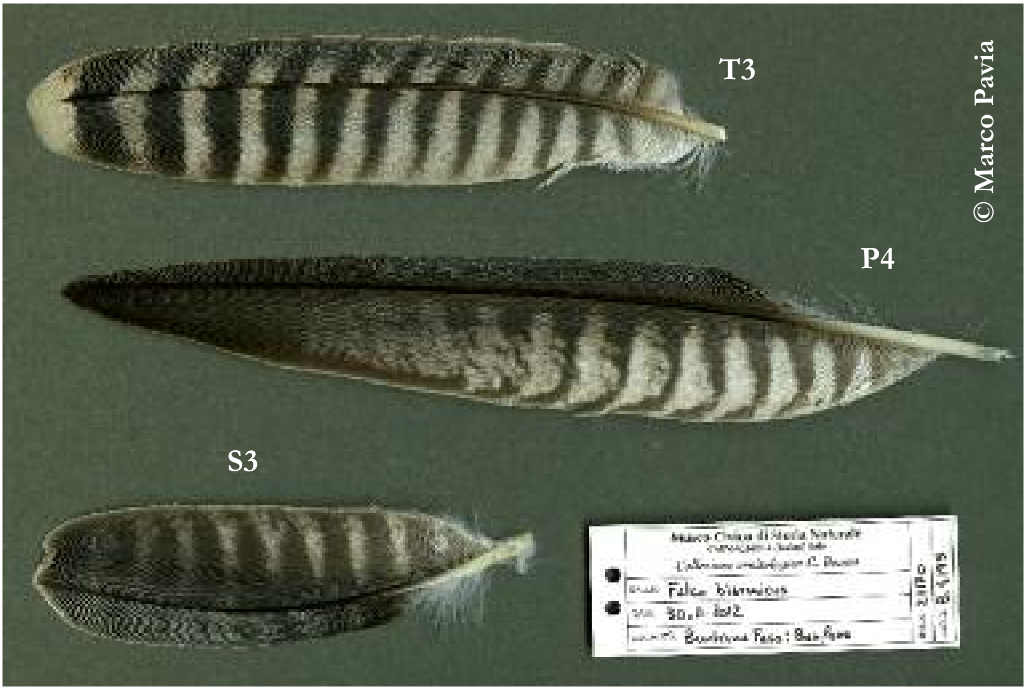


Figure s9 Feathers of an adult *F. b. abyssinicu*s (Cascade Region, Burkina Faso). © and courtesy of Marco Pavia.

Figure s10 Tail and secondary feathers of adult *F. b. feldeggii* (eastern Sicily, Italy). © Giovanni Leonardi.

Sub-adult plumages

In common with other falcons, the Lanner falcon has age-specific plumage morphs. As mentioned above, sub-adult individuals have reached adult morphology in all other respects (i.e. weight, size) and are sexually mature (Kemp 1975, Stephenson 2001). Thus, these plumage displays do not represent an ontogenetic transition toward definitive plumage (Hill 2007). Although plumage maturation is under genetic control, sub-adult plumages encode information about age and breeding status and act primarily as signals in competitive breeding contexts (Dale 2006, Hill 2007).

The chick is covered in white down washed with a pale pink-brown, the skin is pink, and the eyelids pale blue-grey. The culmen is pink, the legs pale orange and the claws light grey (Figure 2.18 A, Figure s11; Kemp 1975). At four days old, the bill becomes grey around the tooth, the skin of the abdomen and anus turns orange and the eyes turn brown (Kemp 1975). At eight days, the second down is apparent on the abdomen, thighs, wings and back whereas dark areas are apparent on the mantle and scapulars (Kemp 1975). The bill turns grey, the legs blue-grey and the toes dull yellow (Kemp 1975). At between 17 and 23 days old several feathers emerge from under the down: body feathers (17 days), rictal bristels (19 days), rectrices and remiges (21 days) and scapulars show as a dark V-shape on the back (23 days old; Figure s12; Kemp 1975). The breast is completely covered at 28 days old and at 35 days the nestling is well feathered but with short tail and wing feathers with some down still adhering to the feather tips (Figure 2.18 B, Figure s16; Kemp 1975). Finally at around 50 days old, any remaining down has disappeared and the complete development of rectrices and remiges is attained (Figure 2.18 C; Kemp 1975). This description of development in *F. b. biarmicus* chicks matches that of *F. b. feldeggii* which follows a similar pattern. In *F. b. feldeggii* sp. body feathers appear at 15 days, rectrices and remiges at 22 days, darker plumages at 26 days and uniform brownish upperparts, barred underparts, grey legs and cream tail covers at 35 days old (Salvo 1984).

As has been observed in young Gyrfalcons, the rusty coloration of the plumage of *juvenile* Lanner falcons is due to the presence of pheomelanin, one of the two main chemical forms of melanin (Galván and Jorge 2015). The synthesis of pheomelanin represents a consumption of cysteine which has a fundamental role in combating environmental factors that generate oxidative stress, such as extreme temperature or parasites (Galván and Jorge 2015). It thus represents an important function during a crucial life phase before the young birds attain adult condition.

Most *juveniles* are not separable to races in the field especially those belonging to the North African races (*F. b. erlangeri* and *F. b. tanypterus*) that, in turn, tend to be somewhat paler than *F. b. feldeggii* sp. (Clark 1999, Corso 2000; Figure 2.19). Overall, *juveniles* that leave the nest and first-winter individuals are almost identical (Corso 2000).

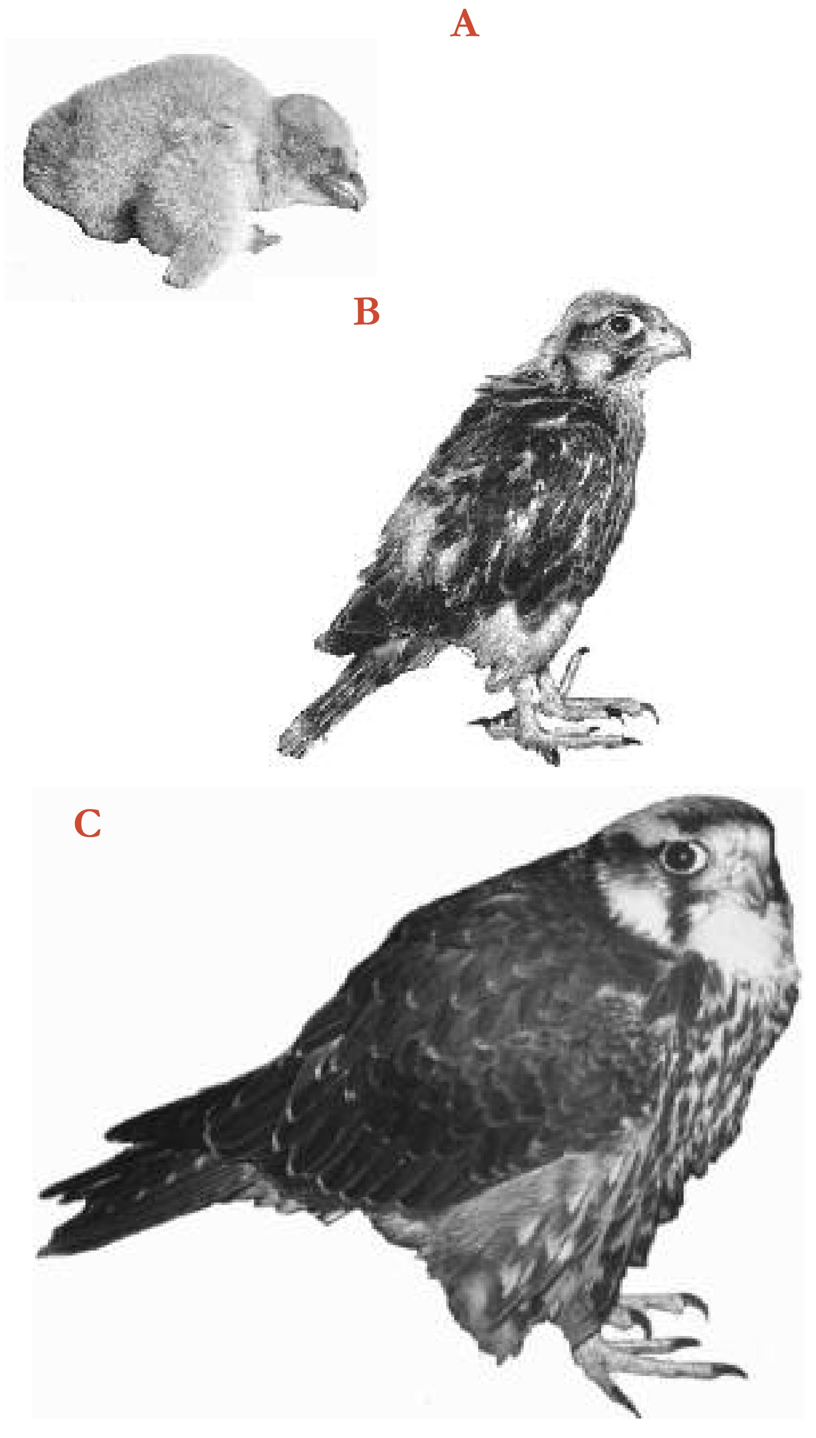


FIGURE 2.18 Stages in the development of a Lanner falcon chick (*F. b. biarmicus*) at successive age: (A) four days old, (B) 31 days old and (C) >35 days old (© and courtesy Alan C. Kemp).

FIGURE S11 A disused crows nest on an electricity pylon in South Africa containing three *F. b. biarmicus* chicks. © and courtesy of Alan C. Kemp.

FIGURE S12 A *F. b. feldeggii* chick of around 20–23 days old, handled as part of a research project in eastern Sicily (Italy) during 2003–2006. © and courtesy of Antonio Brogna.

FIGURE S13 Illustration of the underparts of a *juvenile F. b. feldeggii* in eastern Sicily, Italy. © and courtesy of Mirko Amato.

FIGURE S14 Dorsal view of a *juvenile* female *F. b. biarmicus* in Limpopo province, South Africa. © and courtesy of Malcolm Wilson.

FIGURE S15 A *juvenile* male *F. b. erlangeri* at Auserd in the Western Sahara, Morocco. © and courtesy of Carlos Nazarios Gonzales Bocos.

FIGURE S16 Three 35 day-old *F. b. feldeggii* young, ready to leave the nest (Sicily, Italy). © and courtesy of Markus Varesvuo.

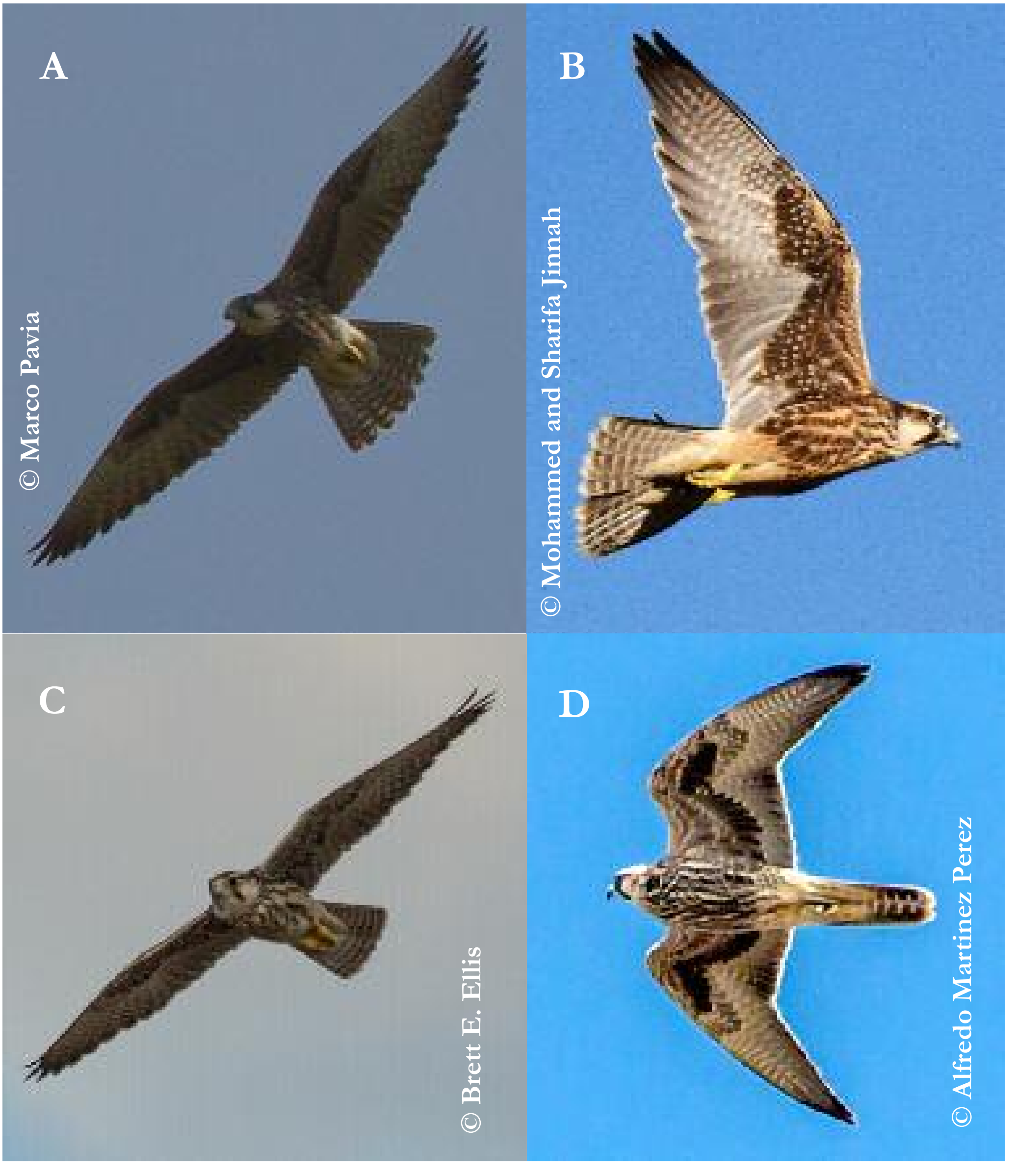


Figure 2.19 *Juvenile* Lanner falcons belonging to different subspecies portrayed in flight. Two common features should be noted: underparts showed a two-toned patterns due a constrast among dark coverts and paler flight feathers and dark streaking ends abruptly on the belly (Clark 1999, Forsman 1999, Corso 2000). In addition, *juveniles* show distinct pale spotting to the underwing coverts (Forsman 1999). Liversidge (1989) proposed the existence of three different *juvenile* types in Southern Africa. (A) *F. b. abyssinicus* Burkina Faso, © and courtesy Marco Pavia, (B) *F. b. biarmicus*, Kgalagadi Transfrontier Park, South Africa, © and courtesy of Mohammed and Sharifa Jinnah (C) *F. b. biarmicus*, Kgalagadi Transfrontier Park, South Africa, © and courtesy of Brett E. Ellis, (D) *F. b. erlangeri*, Strait of Gibraltar © and courtesy of Alfredo Martinez Perez.

Uppersides are dark brown (Figures s14-s18) but Finch-Davies (1920) reported a *juvenile F. b. biarmicus* sp. with upperparts barred with whitish bars. The crown is buffy to dark brown (*F. b. feldeggii*; Figure s16) or whitish on *F. b. erlangeri* and *F. b. tanypterus* (Clark 1999, Forsman 1999), cheeks white with thin black stripes (Figure s16; Chiavetta 1982), and the moustache is long narrow and black, distinguishable from that of the Peregrine falcon (Figure s16; Andreotti *et al.* 2007). In very few cases (*n* = 4) *F. b. feldeggii juveniles* showed a very pale *F. b. erlangeri*-like crown (Massa *et al.* 1991).

The tail is dark brown with numerous incomplete rufous-buff bands with the central pair if feathers often less banded (Figure s17) or generally unbanded (Clark 1999, Chiavetta 1992; Figure s14); the tips of tail feathers show a pale terminal band (Figures s14, s17; Clark 1999, Corso 2000). Adults also have this pale band but it is much narrower and therefore not so visible in flight (s1; Corso 2000). Some individuals can have ovals or spots on their tails (Clark 1999). Wingtips fall short of tail tip by 2-6 cm on perched birds (Clark 1999, Forsman 1999, Corso 2000). A reliable difference when compared with *juvenile* Peregrine falcons is that the pattern of the undertail feathers are uniform and not barred in the Lanner falcon (Corso 1999, Andreotti *et al.* 2007).

Cere and eye-ring remain blue-grey for longer than the legs (Chiavetta 1992, Corso 2000; s13, s14, s16, s17, s18) which turned yellow earlier. Corso (2000) noted that legs become yellowish-grey in summer of the first calendar year and dull yellow around October to December, along with the cere (see Figure s15).

Fresh *juveniles* have pale-grey legs (see s13, s18) as do chicks (s12), but they can also sometimes be yellow (s11). In fact, as mentioned above (*cf.* 1.2 and references therein), leg colour should a large degree of variation among nests but also between members of the same brood as a consequence of the amounts of carotenoid present in the bare parts that is in turn dependant on diet (*cf.* 2.3). Claws are black (Chiavetta 1992).

The second winter plumage on *F. b. feldeggii* show large spots on the breast, barring on the belly and flanks, and a lack of pale cross-barring on feather edges (Clark 1999). Second summer and autumn plumages of *F. b. erlangeri* and *F. b. tanypterus* show heavier spotting on the underparts, a rufous crown, and a narrow dark moustache and eye-line (Clark 1999).

Moult

In spite of the attendant high energy demands, many raptor species, including the Lanner falcon, breed and moult at the same time (Espie *et al.* 1996). The post-breeding moult in adult *F. b. feldeggii* is completed in 132 days from May to September (Chiavetta 1992). The moult for the second calendar year takes as long as for adults whereas *juveniles* make only a partial (body) moult from November (Chiavetta 1992,

FIGURE s17 *Juvenile F. b. tanypterus* in flight (Mount Carmel, Israel). © and courtesy of Eyal Bartov.

FIGURE s18 A *F. b. feldeggii* chick of around 35 days old, handled as part of a research project in eastern Sicily (Italy) during 2003–2006. © and courtesy of Antonio Brogna.

Corso 2000). Average moulting time of primary feathers of captive *F. b. feldeggii* individuals (sequence: 4 – 5 – 6 – 3 – 7 – 2 – 8 – 9 – 1 – 10) takes around 120 days (range 104–146), which is quicker than the same process in the Peregrine falcon (*n* = 8, Figure 2.21; Mebs 1960). The wing moult begins in spring with P4 and P5 (Figure 2.20). No cases of supernumerary primary feathers have been reported (*F. b. tanypterus*; Clark *et al.* 1988).

Species that exhibit strong sexual dimorphism (i.e. RSD) tend to have different energy costs in parental care so the two sexes would also be expected to exhibit different moult patterns (Espie *et al.* 1996, Steenhof 2006). Primary moult in females of *F. b. biarmicus* starts from the first week of September and in the second half of January P7 is still emerging (Kemp 1993). Adult males of the same subspecies start to moult from the first half of November (P4) to the first half of May (P9 completed; Kemp 1993). Thus, as noted by Kemp (1993), females complete their moult before males. In fact in South Africa, breeding females started their moult towards the end of the brooding period but males only started at around the time that the young were beginning to hunt for themselves (Kemp 1993). It is possible that males delay moult to avoid the loss of manoeuvrability and flight performance when there is a need to provide prey to incubating mates (Steenhof 2006). In captivity, breeding females began to moult just after the second egg was laid (Snelling 1973) although moult in captive birds may vary greatly those in the wild (Mebs 1960).

The moult of the secondaries begins shortly before or simultaneously with that of the primaries, although they tend to take a little longer to develop. The secondary

Figure 2.20 Adult male (*F. b. biarmicus*) wing moult (South Africa). The moult score for this bird, starting from P1 (inner), is 00445542000 (0 = old, 4 = nearly completed, 5 = newly completed, 2 = just emerged, 10 primaries in total). This bird started its moult radially at P5, then it had to complete moulting its outer three old primaries and two inner primaries (© and courtesy of Malcom Wilson).

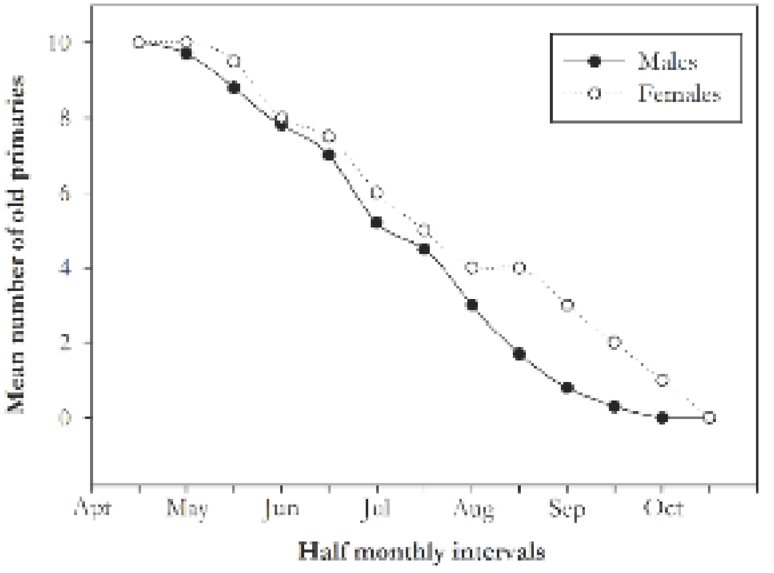


FIGURE 2.21 The mean number of old primaries present during the moulting season for captive male and female Lanner falcons (*F. b. feldeggii*; males = 6, females = 2; Mebs 1960).

moult sequence is 5 – 6 – 7 – 4 – 8 – 9 – 3 – 10 – 2 – 11 – 1 which lasted around 132 days in captive birds (Mebs 1960). In October, two adult males *F. b. biarmicus* in Zimbabwe were seen to have all new secondaries but one of these individuals showed a deformed S3 feather (Mundy and Hartley 2002).

The tail feathers are replaced in the following order: 1 - 2 - 6 - 3 - 4 – 5. The T6 feather moulted almost one week after the second turned out (once even 1 day in advance), the moult completing in around 75 days in captive birds (Mebs 1960). In Zimbabwe, tail feathers in birds observed in October are all old but in December only T5 remained unmoulted (Mundy and Hartley 2002). The rump, wing coverts and back were partially moulted on an immature bird recovered in May (Mundy and Hartley 2002).

Few data are available with regard to moult in other races. In mid-March, single *juveniles* of *F. b. abyssinicus* sp. were observed in moult at Sana'a North Yemen (Cornwallis and Porter 1982). In South Sudan, in individuals of *F. b. abyssinicus*/*F. b. tanypterus* the complete moult took place in midsummer (Lynes 1925). In Saudi Arabia for *F. b. tanypterus* sp. primary wing feathers moulted from March until October and tail feathers from April to October. Adult and *juvenile* birds in Egypt and Israel start the complete moult in around March or April and end in late summer (Forsman 1999). An adult male *F. b. abyssinicus* captured in Burkina Faso showed a complete moult in November (Figures 2.11 and 2.12; M. Pavia pers. comm.). None of the primaries (20) and tail (10) feathers of a seventeen year old male *F. b. biarmicus* were in moult but one secondary feather of the left wing was growing and three ones of the right wing were deformed (Mundy and Hartley 2002).

Bare parts

The bare parts in the Lanner falcon during the first 35 days after hatching show different rates of development. The tarsus (as well as the ulna) were completely developed in 30 days and the culmen, wing and tail in 35 days (Kemp 1975). The cere and the eye-ring begin grey and turn a yellowish-grey by late spring of the second calendar year, whereas leg colour is not finalised until July or August of the first calendar year (Corso 2000). The iris is dark brown or dark hazel and remain the same at all ages, a trait which is common to all races (Sharpe 1904, Forsman 1999). The beak is bluish at the centre, black at the tip, and yellowish at the base (Gurney 1862). Tarsus and feet are pale to bright yellow (Gurney 1860, Stark and Sclater 1900).

Allen's Rule states that birds living in colder regions will have shorter beaks, legs, and wings than relatives in warmer regions (Symonds and Tattersall 2010). In several bird species, the observed strong significant relationships between bill length and environmental temperature seemed to lead to greatly improved thermoregution (Symonds and Tattersall 2010). Despite these findings, no statistical differences between bill length or other bare parts are apparent when comparing measurements between Lanner falcon subspecies (Tables 2.18-2.21). This would seem to contradict Allen's rule, and is similar to observations in other raptor species where no significant differences between the relative size of bare parts exist between subspecies of other falcons from different hemispheres such as the Merlin and Peregrine (Temple 1972, Johansson *et al.* 1998).

This apparent contradiction may be due to the fact that falcons tend to use their

Mean	Sex	Age	n	SD	Range	Reference
51.9	M	ad	6	2.20	48.5 - 55.3	Massa *et al.* 1991
49.1	M	ad	9	4.31	42.5 - 55.0	Chiavetta 1992
51.0	M	ad	2	1.00	50.0 - 52.0	Cramp and Simmons 1980
50.2	M	juv	6	3.50	44.0 - 50.0	Martorelli 1911
53.7	F	ad	16	2.60	49.2 - 58.0	Massa *et al.* 1991
52.9	F	ad	10	4.37	46.0 - 60.0	Chiavetta 1992
54.6	F	ad	7	1.13	53.0 - 56.0	Cramp and Simmons 1980
53.5	F	juv	9	2.45	50.0 - 57.0	Martorelli 1911

Table 2.18 Tarsus measurements of *F. b. feldeggii* sp.

Mean	Sex	Age	n	SD	Range	Reference
49.7	M	ad	2	0.70	49.0 - 50.4	Massa *et al.* 1991
48.7	M	ad	3	1.53	47.0 - 50.0	Whitaker 1905, Martorelli 1911, Hartert 1912
53.0	F	ad	2	2.00	51.0 - 55.0	Massa *et al.* 1991
53.5	F	ad	2	3.53	51.0 - 56.0	Whitaker 1905, Martorelli 1911, Hartert 1912

Table 2.19 Tarsus measurements of *F. b. erlangeri* sp.

Mean	Sex	Age	n	SD	Range	Reference
51.6	M	ad	18	1.54	49 - 55	Cramp and Simmons 1980
52.0	M	ad	3	2.70	52 - 55	Dresser 1871-1881, Martorelli 1911
54.3	F	ad	9	1.66	52 - 57	Cramp and Simmons 1980
54.0	F	ad	2	2.82	52 - 56	Dresser 1871-1881, Martorelli 1911

Table 2.20 Tarsus measurements of *F. b. tanypterus* sp.

Mean	Sex	Age	n	SD	Range	Reference
51.0	M	ad	2	6.64	46 - 55	M. Wilson and M. Parker unpubl. data
48.3	M	*	20	3.37	-	Jenkins 1995
-	M	ad	9	-	45 - 55	MacLean 1984
49.7	M	ad	3	2.31	47 - 51	Mundy and Hartley 2002
52.0	M	juv	12	2.80	48.0 - 54.4	M. Wilson and M. Parker unpubl. data
45.0	M	juv.	4	4.10	42 - 51	Mundy and Hartley 2002
51.9	F	ad	3	0.10	51.8 - 52.0	M. Wilson and M. Parker unpubl. data
52.2	F	*	21	3.80	-	Jenkins 1995
-	F	ad	7	-	45 - 53	MacLean 1984
47.0	F	ad	1			Mundy and Hartley 2002
54.0	F	juv	5	0.90	53 - 55	M. Wilson and M. Parker unpubl. data
48.0	F	juv	2	1.41	46 - 48	Mundy and Hartley 2002

Table 2.21 Tarsus measurements of *F. b. biarmicus* sp.

beaks for killing and dismembering prey through peculiar musculoskeletal characteristics producing the bite forces that might be required for dispatching prey (Sustaita 2008). In common with most perching birds including Passerines and Falcons, the Lanner falcon shows an anisodactyl toe with the inner toe shorter, and this is more pronounced in the Lanner than that in the case of the Peregrine falcon (Mirabelli 1982). It is also worth noting that Jenkins (1995) found some significant differences

Figure 2.22 The relatively long toes of an adult Lanner falcon *F. b. biarmicus* sp. (Kgalagadi Transfrontier Park, South Africa). © and courtesy of Theuns Naude.

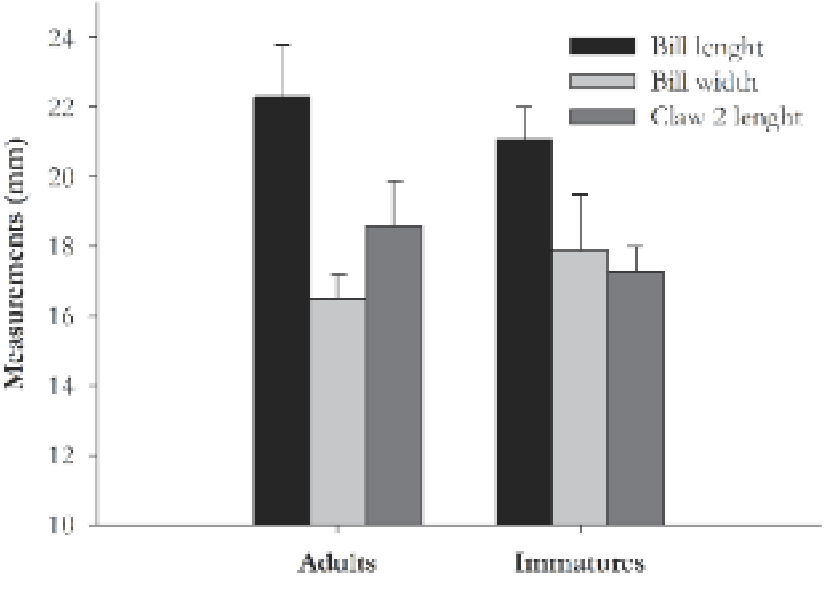


Figure 2.23 Differences in bare part measurements between adult and immature female Lanner falcons (*F. b. biarmicus*; Jenkins 1995).

Suspecies	Bill lenght	Toe 2 (inner toe)	Claw 4
feldeggii	20.3 ± 0.42 (M)	43.2 ± 0.8 (M)	19.3 ± 0.9 (M)
	22.0 ± 1.11 (F)	46.8 ± 1.4 (F)	21.4 ± 1.23 (F)
feldeggii	19.6 ± 0.9 (M)	45.7 ± 1.5 (M)	-
	22.2 ± 1.0 (F)	49.8 ± 3.1 (F)	-
feldeggii	20.2 ± 0.58 (M)	-	-
	22.8 ± 1.09 (F)	-	-
erlangeri	19.0 ± 1.22 (M)	-	-
	21.9 ± 0.64 (F)	-	-
erlangeri	18.9 ± 0.2 (M)	42.5 ± 1.8 (M)	-
	21.4 ± 0.9 (F)	45.7 ± 2.5 (F)	-
tanypterus	19.3 ± 1.0 (M)	42.9 ± 1.26 (M)	18.4 ± 0.95 (M)
	21.8 ± 0.93 (F)	46.9 ± 1.07 (F)	20.9 ± 0.89 (F)
biarmicus	19.3 ± 1.0 (M)	43.4 ± 2.1 (M)	18.3 ± 0.8 (M)
	22.3 ± 1.5 (F)	45.3 ± 2.8 (F)	20.0 ± 1.0 (F)
biarmicus	19.3 ± 0.5 (M)	43.4 ± 3.4 (M)	-
	20.7 ± 0.6 (F)	47.7 ± 0.6 (F)	-

Table 2.22 Bare parts measurements of different Lanner falcon subspecies. There are insufficient data for *F. b. abyssinicus* sp. (two records 24-24.5 mm, adult females in Ethiopia; Friedman 1930). M = Male, F = female (Cramp and Simmons 1980, Massa *et al.* 1991, Chiavetta 1992, Jenkins 1995, Mundy and Hartley 2002).

between adult and immature of *F. b. biarmicus* . In particular, young males have longer tail whereas adult females have larger bill (both length and width) and above all larger second toe (Figure 2.23; Jenkins 1995).

Other bare parts measurements include bill height (mm) of *F. b. feldeggii* (15.8 ± 0.5 Male, 17.4 ± 0.3 female), *F. b. erlangeri* (15.0 ± 1.0 Male, 16.4 ± 0.5 Female) and *F. b. biarmicus* (15.2 ± 1.9 Male, 16.5 ± 0.7 Female) (Massa *et al.* 1991, Jenkins 1995). Finally, some measurements recorded for *F. b. biarmicus* only (Bill depth: 14.7 ± 0.5 Male, 16.2 ± 0.7 Female; Tarsus width: 6.0 ± 0.3 Male, 6.8 ± 0.4 Female; Toe 1: 25.7 ± 3.2 Male, 25.8 ± 4.0 Female; Toe 3: 29.2 ± 3.3 (M), 32.0 ± 3.5 (F); Toe 4: 20.4 ± 2.3 (M), 22.3 ± 1.6 (F); Claw 1: 16.7 ± 1.3 (M), 18.5 ± 1.0 (F); Claw 2: 16.2 ± 0.6 (M), 18.6 ± 1.3 (F); Claw 3: 15.2 ± 0.9 (M), 16.5 ± 1.1 (F) (Jenkins 1995).

Weights

Very few data exist regarding weight for the Palearctic races and none at all for *F. b. abyssinicus*. Glutz *et al.* (1971) quoted Mebs and reported a range of 500–600g for males and 700–900g for females of *F. b. feldeggii* (captive Sicilian birds). Mirabelli

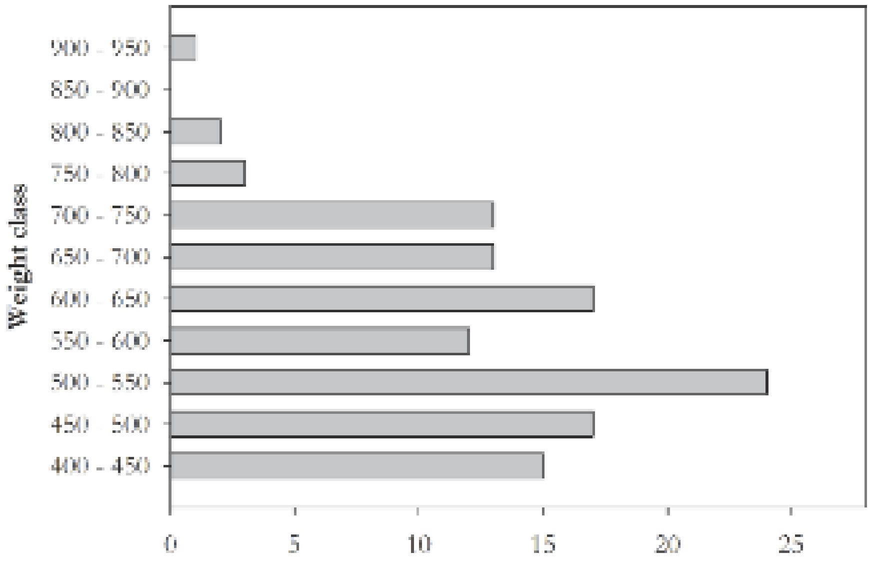


Figure 2.24 Frequency of body weights in Southern African Lanner falcon populations (*F. b. biarmicus* sp.; *n* = 117; Gurney 1862, Langford 1912, Britton 1970, Biggs *et al.* 1979, Cordingley 2009, Dowsett 2009, Mundy and Hartley 2002, M. Parker and M. Wilson pers. data).

(1982) reported weight ranges of 450-560g and 630-825g for males and females respectively in Calabria, southern Italy (*n* = 25 *juveniles* and 12 adults). Other individuals of *F. b. feldeggii* for which weights have been reported include a male of 565g, a female of 830g and a bird with an exceptional weight of 1050g (Chiavetta 1992). Weights of *F. b. erlangeri*/*F. b. tanypterus* races include measurements of males from desert areas in Chad (442g) and Algeria (552g) and means for males (550g) and females (800g) from the Middle East. Clark (1999) pooled the available data for all Palearctic races and found that weights for males ranged from 450 to 650g (average: 550g) and females from 550g to 800g (650g).

Data from a total of 86 individuals of the nominate *F. b. biarmicus* can be gathered from a combination of published studies and unpublished data, much of it collected mainly in Southern Africa (Figure 2.24). A male seventeen year old wild Lanner falcon was reported as weighing 348g, which is at the lower end of the minimum values (Mundy and Hartley 2002). A significant difference exist between genders (Figure 2.25) but none is apparent between adults and young of various ages (Stephenson 2001, M. Parker and M. Wilson pers. data). In fact, according to Jenkins (1995) and Stephenson (2001), body mass alone is not a sufficient characteristic to reliably discriminate between *juvenile* and adult birds.

Differences among sexes

In common with other *Falco* species, the Lanner falcon show a strong Reverse Size Dimorphism (RSD), females being larger than males both in structure and flight apparatus (Tables 2.23 and 2.26; Krüger 2005). One study found that males of *F. b. biarmicus* sp. were on average, by body mass, 73% the size of females (Stephenson 2001). This value is very close to the 71% calculated from a comprehensive dataset that included 52 individuals (Figure 2.25).

A reliable measure of RSD could be calculated by dividing the wing length of males by the wing length of females, with this ratio subsequently cubed to estimate differences in bulk and flight performance (Krüger 2005). Applying this formula across all races of the Lanner falcon, the RSD ranged from 0.79 in *F. b. tanypterus* and *F. b. abyssinicus* to 0.83 in *F. b. feldeggii* and *F. b. biarmicus* (Figure 2.27). Generally, species that exhibit strong RSD tend to hunt larger and more agile prey and this specialisation might have evolved in order to allow more efficient foraging (Krüger 2005). In fact, in common with other raptor species, these results show that hunting method was negatively correlated with RSD whereas sexual plumage dimorphism was positively correlated with RSD, indicating that the species showed smaller plumage differences between the sexes (Krüger 2005).

Although Corso (2000) reported some of these differences in plumage patterns

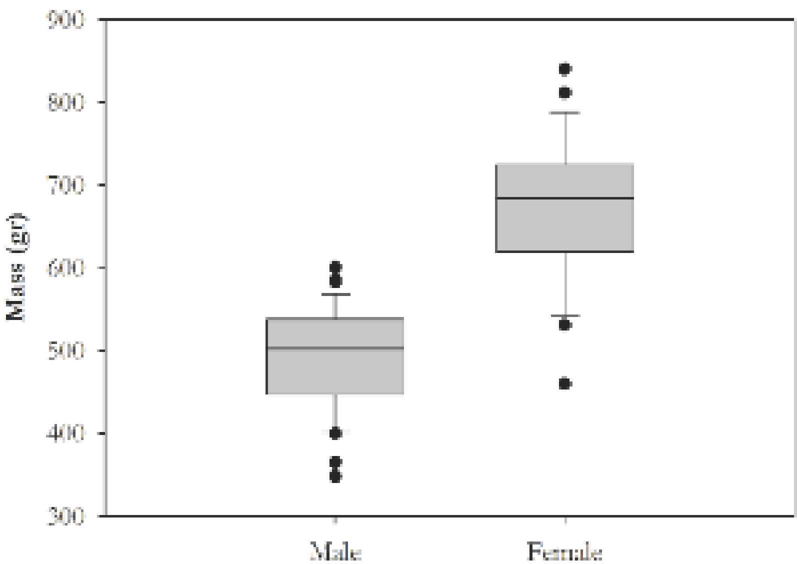


FIGURE 2.25 Differences of body weights between male and female Lanner falcons (*F. b. biarmicus*; $n = 52$; Gurney 1862, Langford 1912, Britton 1970, Biggs *et al.* 1979, Cordingley 2009, Mundy and Hartley 2002, M. Parker and M. Wilson pers. data).

Measure (±SD)	Male	Female	Sign.
Wing area	1050.4 (172.7)	1262.40 (100.24)	$p<0.005$
Body mass (g)	520.3 (71.5)	594.92 (43.0)	$p<0.005$
Linear loading	0.251 (0.02)	0.237 (0.010)	$p<0.01$
Mass loading	0.508 (0.07)	0.474 (0.047)	n.s.
Wing length (mm)	305.7 (9.9)	341.1 (16.8)	$p<0.005$
Secondary length (mm)	154.2 (3.31)	176.50 (6.84)	$p<0.005$
Ulna length (mm)	95.67 (2.55)	103.25 (3.54)	$p<0.005$
Wing area index	618.94 (23.02)	784.68 (49.26)	$p<0.005$

Table 2.23 Differences between male and female Lanner falcons *F. b. biarmicus* sp. (n = 35). Linear loading is the cube root of mass divided by the square root of wing area. Mass loading is body mass divided by wing area and wing area index is wings span^2/wing area (Mendelsohn *et al.* 1989).

between males and females in *F. b. feldeggii*, he found no strong relationships that allowed the distinction of traits between sexes due to RSD (Clark 1999, Forsman 1999, Krüger 2005). The presumed enhanced foraging efficiency of males is based on wing length and especially on tail length, characteristics that allow for more manoeuvrability during hunting flights (Wiklund 1996). Interestingly, tail/wing ratios of the Lanner falcon races show significant differences between the sexes only for *F. b. feldeggii* (Mann-Whitney U Statistic = 57.500; p = <0.001) and *F. b. erlangeri* (p = 0.003) but not for *F. b. tanypterus* (p = 0.079) and *F. b. biarmicus* (p = 0.225). In addition, male *F. b. biarmicus* sp. had relatively heavier loads than females, and was the only Southern African raptor species to show any sexual difference in wing loading (Table 2.23; Mendelsohn *et al.* 1989).

The intrasexual competition hypothesis states that RSD is maintained by the higher competitive ability of larger females to secure higher quality territories, to increase mortality of larger immature males, and hence to obtain greater breeding success (McDonald *et al.* 2005). In fact, McDonald *et al.* (2005) found inside a breeding population of Brown falcon (*F. berigora*) a strong relationship between body size and recruitment rate in adult females but also a severe decrease in survival in larger immature males. Unfortunately, there are insufficient data on recruitment from breeding pairs of Lanner falcons, as well as survival rates in young (Leonardi 2001). Nevertheless, where RSD become evident such as for *F. b. feldeggii* sp. (Figure 2.10) a persistent number of unpaired birds each season and the absence of instant recruits could lend some support to the intrasexual competition hypothesis (Mirabelli 1982, Leonardi *et al.* unpubl. data). High degrees of mortality amongst immature birds is also plausible given the absence of recoveries of ringed fledglings and the limited number of high quality nesting sites that would in turn greatly improve pro-

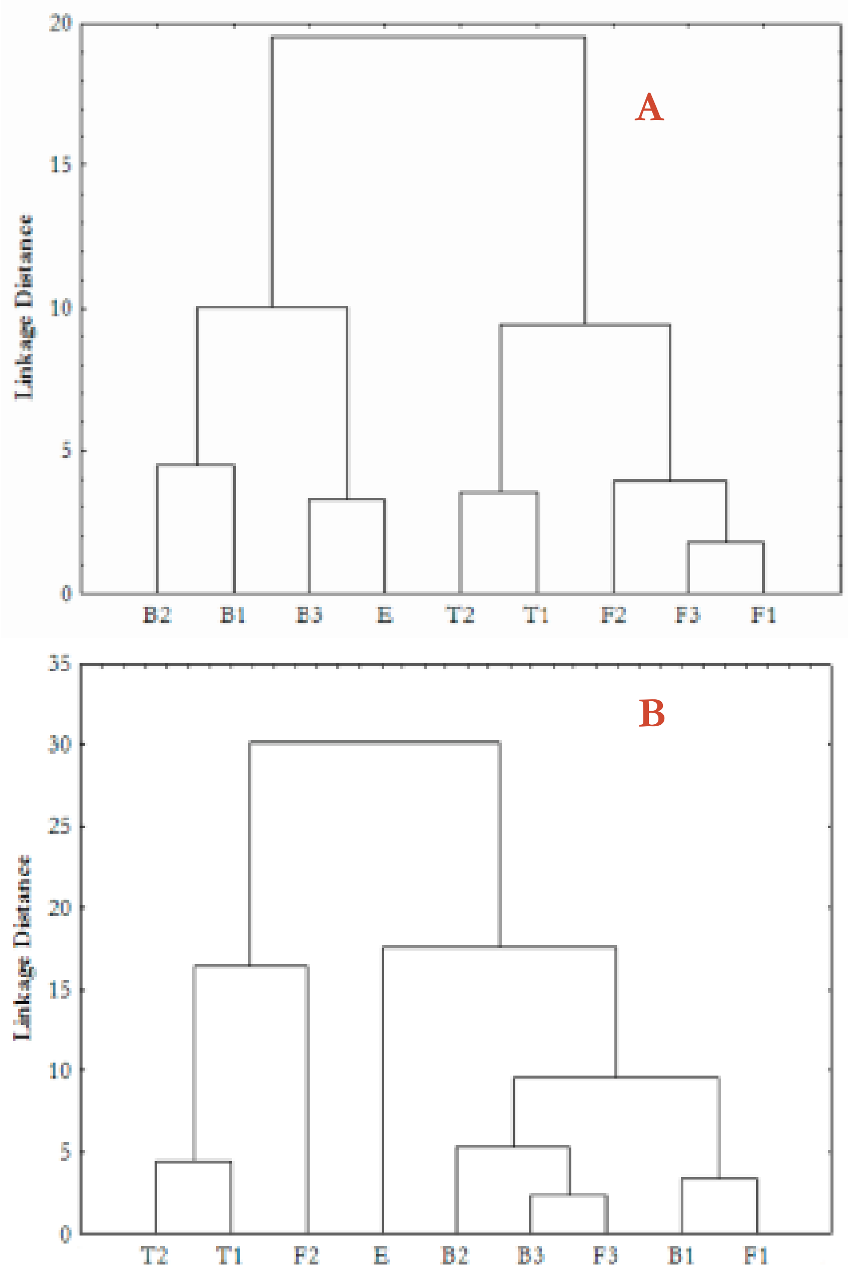


FIGURE 2.26 Unrooted NJ (Neighbor-Joining) trees based on squared Mahalanobis distance, and calculated with three morphological variables (wing, tail, tarsus length). Due to strong reverse size dimorphism between male and female Lanner falcons data were split by sexes (A = males, B = females). Subspecies: F = *F. b. feldeggii*, E = *F. b. erlangeri*, T = *F. b. tanypterus*, B = *F. b. biarmicus*. Sample datasets: F1 (Massa *et al.* 1991), F2 (Chiavetta 1992), F3 (Cramp and Simmons 1980), E (Massa *et al.* 1991), T1 (Cramp and Simmons (1980), T2 (see Tables 2.7, 2.13, 2.22), B1 and B3 (M. Wilson and M. Parker unpubl. data), B2 (Jenkins 1995).

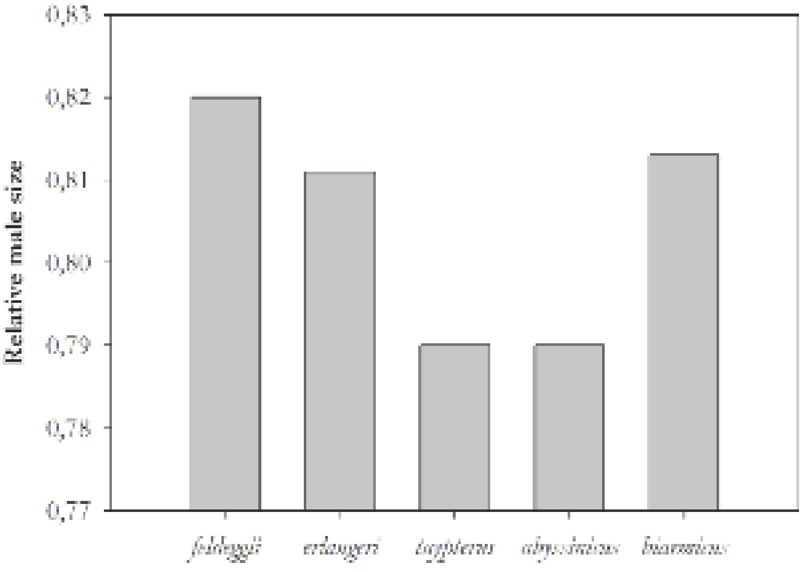


FIGURE 2.27 The distribution of RSD (measured as cubed wing length ratios)between the Lanner falcon races. Data derived from Tables 2.6-2.10.

ductivity (Cipriano 2005, Amato *et al.* 2014).

An in-depth analysis is possible using some morphological traits such as wing, tail and tarsus length found in the published literature. As mentioned above there are unfortunately not enough data available for the *F. b. abyssinicus* race for this purpose. The PCA analysis revealed that around 70% of variability accounted for males was derived from wing and tail lengths that split the subspecies into two main groups (Figure 2.26 A). Different samples of *F. b. feldeggii* (Cramp and Simmons 1980, Massa *et al.* 1991, Chiavetta 1992) and *F. b. tanypterus* sp. (Cramp and Simmons 1980, several Authors cited in Tables 2.7 and 2.13) combined to form the first group (Figure 2.26). The other group consists of all *F. b. biarmicus* sp. samples (Jenkins 1995, Mundy and Hartley 2002, M. Wilson and M. Parker unpubl. data) along with some of *F. b. erlangeri* included (Massa *et al.* 1991; Figure 2.26).

As with males, wing, tail and tarsus measurements accounted for a great portion of variability of female samples but the figure was slightly less in females than in males at around 60% (Figure 2.26 B). The NJ tree again shows several main groupings: the first one with *F. b. tanypterus* and *F. b. feldeggii* samples and the second with *F. b. erlangeri* (separated) and two sub-groups with all *F. b. biarmicus* and the remainder *F. b. feldeggii* samples (Figure 2.26 B). These results confirm the relationships between *F. b. feldeggii* and *F. b. tanypterus* and also between *F. b. erlangeri* and *F. b. biarmicus*, but also reveal a certain similarity among *F. b. feldeggii* and *F. b. biarmicus* females (Figure

2.26 B). These phenotypic traits as well as genetics (*cf.* 1.5) and fossils (*cf.* 1.1) are parts of the comparative framework for the identification of macro-distributional areas of the Lanner falcon (see also section 3.2).

2.5 Eggs

Colour patterns

In clutches of Eleonora's and Red footed falcons (*F. vespertinus*), the first eggs to be laid are pale brown with numerous small dots whereas subsequent eggs are dark brown with many dots of larger dimensions (Horváth 1955, Wink *et al.* 1985). Following the '*structural-function hypothesis*', the speckles strengthen the eggshell when calcium is scarce and thus occurs primarily in thinner areas of the shell (Gosler *et al.* 2005). Nevertheless, eggshell colour carries information on intrinsic properties of the female that laid the egg in terms of the concentrations of the two key eggshell pigments, protoporphyrin IX (related to calcium) and biliverdin (Cassey *et al.* 2012). The protoporphyrin pigment concentration were consistently associated with species that lay maculated eggs and nest in cavities, such as falcons (Cassey *et al.* 2012). In addition, protoporphyrin should provide protection to the shell where eggs are laid in particularly humid substrates which make them more susceptible to increased microbial infection (Cassey *et al.* 2012).

Usually eggs of the Lanner falcon are brighter, more yellow than brown, and speckled reddish-brown, especially so in those of *F. b. abyssinicus* and *F. b. erlangeri* (Coltart 1952, Schönwetter 1960). Erlanger (1898) observed a certain variability among clutches collected in North Africa where two breeding sites only (17%) had reddish-brown eggs. In addition, he found a clutch with two yellow-brown eggs and the other one reddish-brown (Erlanger 1898). In a clutch of four found in a nest near the second Pyramid of Giza one egg was marked with purple rather than red (Warthausen 1860). Coltart (1952) noted that some eggs could also be marked with small blotches so that a pinky-cream colour is apparent, more so at the small ends. Intra-clutch variability, in terms of spottiness and background colour, has also been observed in broods of *F. b. tanypterus*, *F. b. feldeggii* and *F.*

FIGURE 2.28 An unfertile egg of the Lanner falcon (*F. b. feldeggii* sp.). © Giovanni Leonardi.

FIGURE s19 A *F. b. tanypterus* ground nest in the Eastern desert © and courtesy of C. Vance Haynes.

FIGURE s20 Female *F. b. feldeggii* in flight (Sicily, Italy). © and courtesy of Markus Varesvuo.

variability, in terms of spottiness and background colour, has also been observed in broods of *F. b. tanypterus*, *F. b. feldeggii* and *F. b. biarmicus* (Figure s19; Tarboton and Allan 1984, Goodman and Haynes 1989, Massa *et al.* 1991).

As expected, different degrees of variability have been reported in the published literature. For example Whitaker (1905) recognized a high degree of variation in colour and size, but found that in general eggs are pale reddish or yellowish-red covered all over with darker red spots and blotches. Jany (1960) however, found a great deal of similarity in eggs from the same habitat type such as in Serir Tibesti in Libya and in southern Algeria. Coltard (1952) made a description of a clutch of three eggs of *F. b. abyssinicus*. Two of these eggs were finely freckled all over with pinky-brown, with superimposed red-brown blotches at the small ends, while the other egg had a white background with small greyish-pink spots and very few of greyish brown (Coltard 1952).

Overall, several authors distinguish brighter and clearer *F. b. biarmicus* and *F. b. tanypterus* eggs from those of the Peregrine falcon (Figure s19; Warthausen 1860, Coltard 1952, Schönwetter 1960). Warthausen (1860) considered the eggs of the Lanner falcon to be equal in size to those of the Peregrine, but found a difference in structure between the two, with pores in the eggs of the Peregrine less oblong and rather infundibulifor, while those of the Lanner are more distinctly marked and serrated (Figure 2.28). A possible explanation for these structural differences is that eggshells

FIGURE 2.29 A *F. b. feldeggii* nest with two chicks and two eggs checked as part of a research project in eastern Sicily (Italy) during 2003–2006. © and courtesy of Antonio Brogna.

with smaller pores are more capable of retaining water in environments characterised by lower humidity and higher temperatures but no definitive quantitative data on Lanner falcon eggs exist (Stein and Badayev 2011).

Shell thickness, shell mass and egg mass

A review on the thickness of the shells of Lanner falcon eggs was compiled by Schönwetter (1960). These measures were taken mainly from eggs collected before the widespread use of pesticides became common and could therefore be considered as being descriptive of healthy egg condition (see the section on *Pesticides*). Unfortunately, as with other measures, no data are available for the *F. b. abyssinicus* race. Thickness of eggs varied among the races from the thicker egg shells of *F. b. feldeggii* sp. (0.34 - 0.36 mm, n = 10) to *F. b. erlangeri* sp. (0.34 mm, n =50), *F. b. tanypterus* sp. (0.33 mm, n = 40) and *F. b. biarmicus* sp. (0.31 mm, n = 10) (Schönwetter 1960). In addition, these values are very close to those of Saker (0.38 mm), Laggar (0.35 mm) and Prairie falcons (0.35 mm; Schönwetter 1960). Thickness may help to decrease embryo mortality because the risk of trans-shell bacterial infection is greater under conditions of high humidity (Stein and Badayev 2011). Accordingly, eggshell structure ranged from the thicker shells of *F. b. feldeggii* sp. that occupy Mediterranean Europe to the thinner eggs associated with the Namibian-dwelling *F. b. biarmicus* sp. (Schönwetter 1960).

Overall shell mass is positively related to egg mass as well to egg thickness, and ultimately all of these variables are dependant on the availability of calcium (Schönwetter 1960, Morales *et al.* 2013). Using Schönwetter's data on the same clutches of the Lanner falcon, the egg mass seems to have no influence on shell mass (p = 0.067) but shell thickness (p = 0.022). Also, no significant relationships exist between shell mass and thickness (p = 0.128). Unfortunately, other published data are scarce and

Subsp.	Min	Max	Mean	Sites	Reference
feldeggii	3.3	5.8	4.9	Sicily	Massa *et al.* 1991
feldeggii	4.15	4.8	4.5	Greece	Schönwetter 1960
feldeggii	3.49	4.78	4.31	S Italy, Sicily,	Schönwetter 1960
erlangeri	3.0	4.65	3.94	N Africa	Schönwetter 1960
tanypterus	3.86	4.73		Egypt	Warthausen 1860
tanypterus	3.26	4.55	4.15	Sudan, Egypt	Schönwetter 1960
biarmicus	3.3	4.1	3.9	Angola, Namibia	Schönwetter 1960

Table 2.24 Shell mass measures (minimun - maximum and mean in g) of several Lanner falcon populations from different countries.

scattered and do not allow further more detailed comparisons (Table 2.24). Nevertheless, it seems that shell mass is strong related with the length (p <0.001) and the breadth (p <0.001) of eggs hence is related to their relative overall shape and size (Figure 2.30).

Egg masses reported by Schönwetter (1960) are: *F. b. feldeggii* 50g (southern Italy and Sicily) and 48g (Greece), *F. b. erlangeri* 48g (North Africa), *F. b. tanypterus* 48g (Sudan and Egypt), *F. b. abyssinicus* 41g (Nigeria and Eritrea) and *F. b. biarmicus* 41g (Angola and Namibia). MacLean (1984) give the mass of *F. b. biarmicus* eggs in Southern Africa as ranging from 41g to 47g. Very few data have been published regarding the fresh egg mass, but available figures include *F. b. tanypterus* eggs (41.2 ± 0.4; n = 2) produced in captivity and a clutch of three eggs of *F. b. biarmicus* laid in eastern Zambia (which weighed 38.7g, 44.4, and 48.1g; Osborne and Colebrook-Robjent 1984, Tazawa *et al.* 2001).

Egg breadth and length

Egg size varies greatly within many avian species but it appears to be a characteristic of individual females, and yet the traits of a female (including physiological characteristics) that determine egg size are not clearly understood (Christians 2002). For

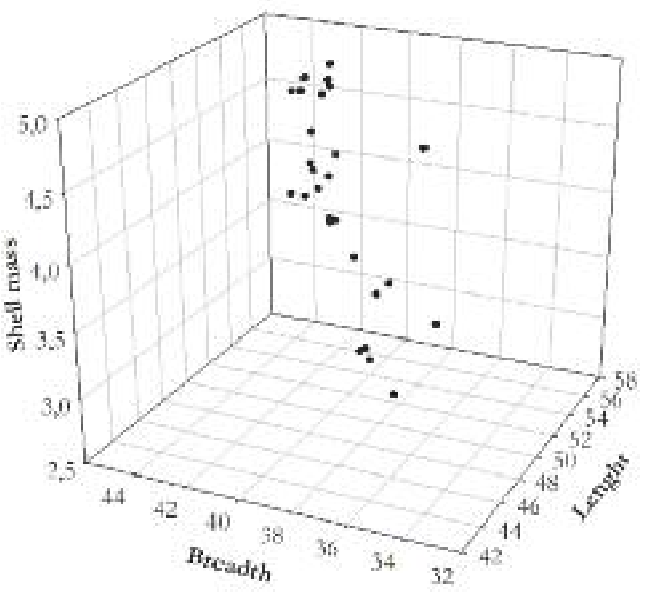


Figure 2.30 The strong positive relationship between shell mass and the breadth and length of the Lanner falcon egg (Warthausen 1860, Schönwetter 1960, Massa *et al.* 1991).

Subsp.	Min	Max	Mean	Sites
feldeggii	38.8 × 48.8	42.4 × 55.3	40.9 × 52.2	Sicily
feldeggii	41.0 × 50.2	42.5 × 53.8	41.6 × 52.2	Greece
feldeggii	38.3 × 50.4	42.5 × 56.2	40.9 × 52.9	S Italy, Sicily, Balkans
feldeggii	39.0 × 47.0	43.0 × 55.0	42.0 × 50.0	Balkans
feldeggii	38.3 × 46.8	42.5 × 56.2	41.0 × 52.0	Europe
erlangeri	43.0 × 45.0	42.5 × 55.0	40.3 × 50.7	Morocco
erlangeri	-	-	39.5 × 51.5	Tunisia
erlangeri	38.4 × 50.0	43.0 × 54.4	40.2 × 51.2	N Africa
tanypterus	37.8 × 53.5	41.6 × 56.0	41.2 × 53.1	Jordan
tanypterus	37.8 × 48.1	44.0 × 56.0	41.1 × 48.8	Sudan, Egypt
tanypterus	32.0 × 41.0	39.6 × 54.9	35.3 × 44.6	Eastern Sahara desert
abyssinicus	37.0 × 45.8	40.0 × 53.0	38.6 × 49.7	Nigeria, Eritrea
biarmicus	39.6 × 47.7	44.6 × 56.6	40.5 × 51.6	Southern Africa
biarmicus	37.7 × 47.3	42.9 × 55.0	40.7 × 52.3	Southern Africa
biarmicus	38.5 × 47.7	44.6 × 56.5	40.5 × 51.8	Southern Africa
biarmicus	42.0 × 55.2	44.0 × 58.3	43.2 × 56.6	E Cape, S Africa
biarmicus	38.6 × 50.0	43.1 × 52.9	41.0 × 51.2	E Zambia
biarmicus	37.7 × 47.3	42.7 × 54.6	40.7 × 51.8	Angola, Namibia

Table 2.25 Length and breadth (min., max. and average) of Lanner falcon eggs of all subspecies (Hartert 1912, Schönwetter M. 1960, Etchecopar and Hüe 1964, Géroudet 1979, Cramp and Simmons 1980, Brown *et al.* 1982, Steyn 1983, MacLean 1984, Osborne and Colebrook-Robjent 1984, Goodman and Haynes 1989, Massa *et al.* 1991, Stephenson 2001).

example, the length, breadth and fresh weight of eggs laid by the same female Peregrine falcon decreased over time (Burnham *et al.* 1984). Nevertheless, egg size has been generally found to be independent of the female's body size, the age or size of her mate, or weather conditions during clutch formation (Wheelwright *et al.* 2012). This may suggest high repeatability of the traits of eggs laid by a particular female which may reflect high heritability of a genetic component (Wheelwright *et al.* 2012).

Table 2.25 summarized egg traits of Lanner falcon subspecies collected in several parts of the distributional area. The egg shape (the ratio of breadth:length) is thought to derive from pressures exerted in the oviduct, without which an elliptical egg would be formed (Troscianko 2014). The mean shape and the coefficient of variation of *F. b. feldeggii* (0.79 ± 0.02 – 3.2%), *F. b. erlangeri* (0.79 ± 0.01 – 1.3%), *F. b. tanypterus* (0.76 ± 0.03 – 3.9%), *F. b. abyssinicus* (0.78 ± 0.02 – 3.1%), *F. b. biarmicus* (0.79 ± 0.02 – 2.5%) eggs show a low variability (Figure 2.31). Thus eggs show a low variation in shape, and they are all relatively elongated (0.76 – 0.79) with a small average coefficient of variation of 2.8%.

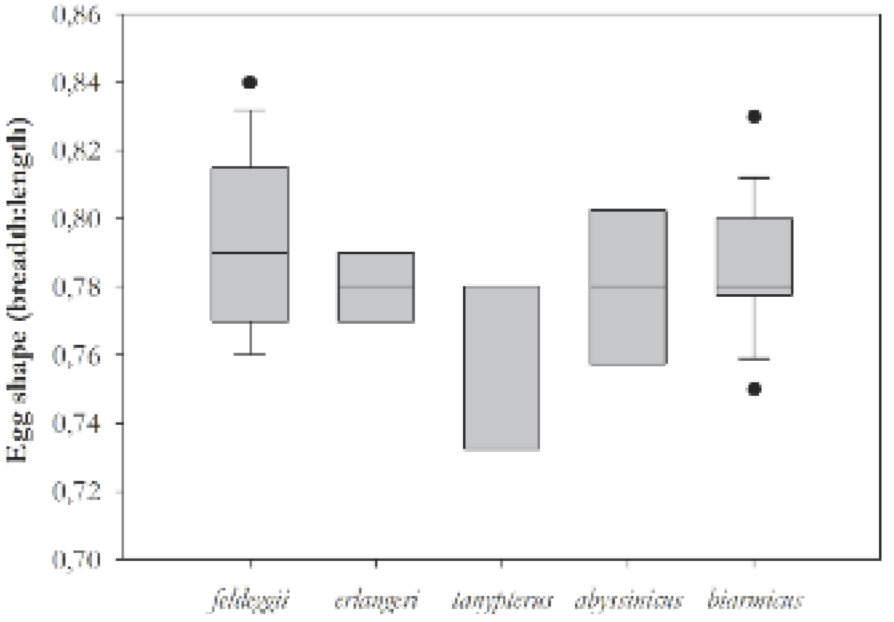


Figure 2.31 Egg shape (breadth:length) of Lanner falcon eggs of all subspecies (Warthausen 1860, Whitaker 1905, Hartert 1912, Paris 1921, Coltart 1952, Schönwetter 1960, Etchecopar and Hue 1964, Géroudet 1979, Cramp and Simmons 1980, Brown *et al.* 1982, Steyn 1983, MacLean 1984, Osborne and Colebrook-Robjent 1984, Massa *et al.* 1991, Stephenson 2001).

Egg measures for a total of 21 clutches have been reported in the literature: 2 of *F. b. feldeggii* (Mebs 1960), 7 of *F. b. erlangeri* (Erlanger 1898, Coltart 1952), 5 of *F. b. tanypterus* (Coltart 1952, Goodman and Haynes 1989), and 11 of *F. b. biarmicus* (Schönwetter 1960, Allan and McInnes 2002). As observed by Wink *et al.* (1985) for the Eleonora's falcon, there is a great degree of variability that characterizes the inter-clutch differences of the Lanner falcon (length p <0.001, breadth p <0.001 and egg shape p = 0.002). These results confirm the importance the of anatomy and physiology of the female on egg traits (Wink *et al.* 1985). The clutch size has no effect on length (p = 0.654), or egg shape (p = 0.169) but does have a slight influence on breadth (p = 0.024). Intra-clutch differences include length (t-test, p = 0.037), breadth (p = 0.072) and a significant link amongst the shape of eggs (p = 0.007). Again, female investment in reproduction will certainly have a fundamental role on egg production (Troscianko 2014).

Egg volume

Measurements of egg length (L) and breadth (B) have been used commonly to estiparticularly by Hoyt's (1979) equation:

$$V = 0.51 \times LB^2$$

Hoyt's volume estimation equation is affected by an error equivalent to 7.7–9.0% of egg volume due to the '*pointedness*' of eggs that lead to overestimating the volumes of elliptical eggs and underestimating the volumes of pointed eggs (Troscianko 2014). Nevertheless without photographic datasets, length and breadth are the most common measures found in published studies, and they are also often used for large scale analysis on egg size (Ruuskanen *et al.* 2011, Wheelwright *et al.* 2012).

As well as for other traits, the eggs of Lanner falcon subspecies do not differ significantly by volumes (Figure 2.32) or by latitude ($p = 0.407$; Ruuskanen *et al.* 2011). Except for *F. b. abyssinicus* eggs (average: 37.8 cm³ SD = 4.6) that are slightly smaller, the volumes of *F. b. feldeggii* (average: 44.6 cm³ SD = 5.5), *F. b. erlangeri* (average: 44.4 cm³ SD = 5.4), *F. b. tanypterus* (average: 44.9 cm³ SD = 7.2), and *F. b. biarmicus* (average: 44.6 cm³ SD = 5.5) eggs are all quite similar. Similarly, the coefficient of variation (SD/mean × 100) was around 12% for *F. b. feldeggii*, *F. b. erlangeri* and *F. b. abyssinicus* eggs and around 16-17% for those of *F. b. tanypterus* and *F. b. biarmicus*.

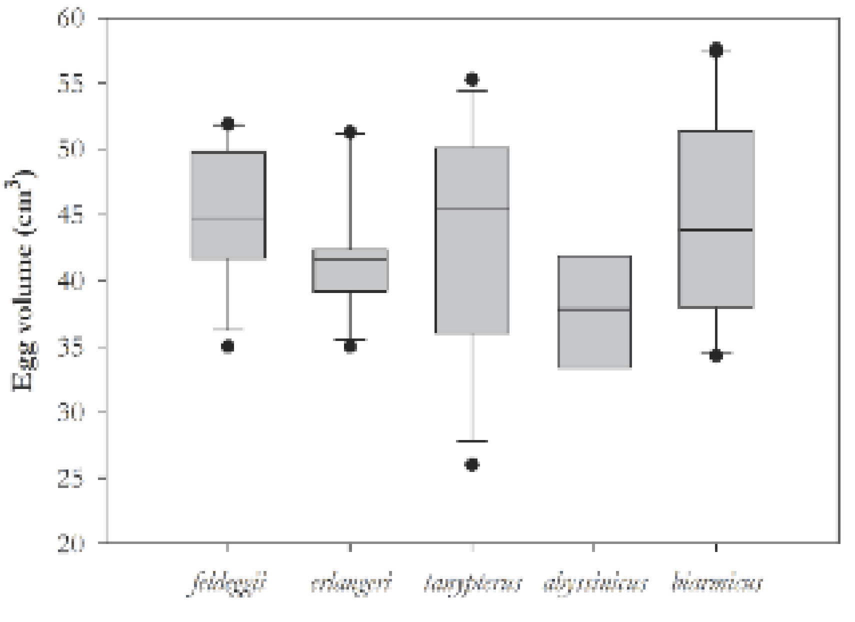


Figure 2.32 Variability of egg volumes of Lanner falcon subspecies (Warthausen 1860, Hartert 1912, Paris 1921, Coltart 1952, Schönwetter 1960, Etchecopar and Hue 1964, Géroudet 1979, Cramp and Simmons 1980, Brown *et al.* 1982, Steyn 1983, MacLean 1984, Osborne and Colebrook-Robjent 1984, Massa *et al.* 1991, Stephenson 2001).

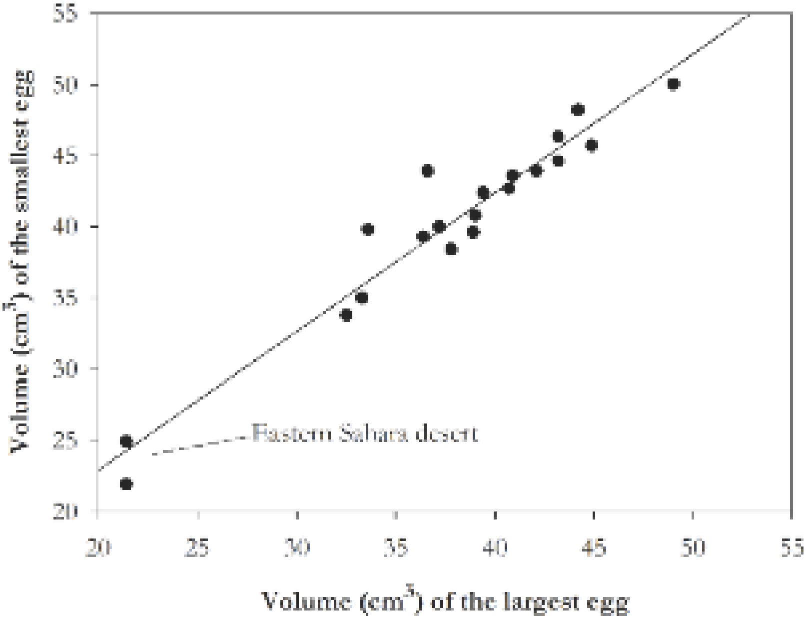


Figure 2.33 The strong relationship among the smallest and the largest eggs inside clutches of the Lanner falcon (Warthausen 1860, Hartert 1922, Paris 1921, Coltart 1952, Schönwetter 1960, Etchecopar and Hue 1964, Géroudet 1979, Cramp and Simmons 1980, Brown *et al.* 1982, Steyn 1983, MacLean 1984, Osborne and Colebrook-Robjent 1984, Goodman and Haynes 1989, Massa *et al.* 1991, Stephenson 2001).

Inter-clutch differences are significant by volumes $p<0.001$ but volumes are not correlated with clutch size ($p = 0.223$). A morphological comparison among the smallest and the largest eggs inside clutches of the Lanner falcon shows a strong positive relationship (Figure 2.33). Thus with regard to the female investment across the entire clutch, the varaibility among egg volumes remains at least constant and showed a directly proportional correlation (Figure 2.33). In other words, females produce clutches strictly limited by their physiological characteristics, such as endogenous protein stores, oviduct mass and the rate of protein uptake by ovarian follicles, that ultimately determines egg size (Christians 2002). In fact, when comparing between females with a similar investment in eggs, it would only be possible to increase clutch size by laying smaller eggs (Nager *et al.* 2000). This is evident for female Lanner falcons of the Eastern Sahara desert that are forced by the extreme conditions and a short period of food availability to lay smaller eggs ($p = 0.005$; see Table 2.25, Figure 2.33; Goodman and Haynes 1989). Additionally from other populations, it has been found that large clutch sizes of three or four eggs usually consist of very small eggs (32.8 × 41 mm) with a mean volume (22.5 cm^3) which can be around more than half of the average (40.9 cm^3).

2.6 Flight performance

Several authors have remarked on the flight of Lanner falcons. Gurney (1862) remarks that '*Their flight is excessively rapid when occasion require, but at other times they appear generally to soar easily and quietly about, apparently well scanning the ground over which they pass*'. Birds of *F. b. biarmicus* sp. are described as being capable of '*very powerful and swift flight*' (Finch-Davies 1920) and as being '*very rapid on the wing, not hesitate in the mists of people working on the farmyard*' (Layard and Sharpe 1897).

Field studies have revealed that flight activities by breeding pairs accounted for 16.8% (South Africa) and 16% (Sicily; range 8% to 25%) of the whole measured time budget (Jenkins 1995, Amato 2004). As expected, peaks of activity correspond to the nesting period when parents made the maximum energy investment (Amato 2004). Jenkins (1995) provides the most complete analysis on the flight performance of the Lanner falcon (*F. b. biarmicus*) and Table 2.26 summarizes these parameters for males and females during both horizontal flapping flights and gliding flights.

Predicted and observed performance confirms that the Lanner falcon is a relatively efficient user of thermals as opposed to the use of powered flapping flights (Jenkins

FIGURE 2.34 A female Lanner falcon (*F. b. feldeggii*) performing a thermal soaring flight, Eastern Sicily. © and courtesy of Markus Varesvuo.

Flight parameters	Male	Female
Horizontal flapping flight		
(a) Minimum power speed (m s^{-1})	8.5 ± 0.2	9.3 ± 0.3
(b) Maximum range speed (m s^{-1})	14.2 ± 0.3	15.3 ± 0.5
(c) Effective lift:drag ratio	8.12 ± 0.24	8.28 ± 0.25
(d) Fuel consumption (g km^{-1})	0.068 ± 0.005	0.098 ± 0.012
(e) Aerobic scope	12.91 ± 0.77	15.20 ± 1.20
Gliding flight		
(f) Stall speed (m s^{-1})	6.52 ± 0.29	7.06 ± 0.30
(g) Best glide ratio	13.9 ± 0.3	14.0 ± 0.4
(h) Best glide speed (m s^{-1})	9.2 ± 0.3	10.0 ± 0.4
(i) Minimum sinking speed (m s^{-1})	0.578 ± 0.026	0.627 ± 0.04
(j) Circling radius (m)	12.2 ± 1.1	14.3 ± 1.3
(k) Cross country speed (m s^{-1})	12.2 ± 0.2	12.9 ± 0.2
Other parameters		
Flight distance index (m)	1469 ± 1083	1263 ± 1202
Flight time (s)	269 ± 274	167 ± 114
Flight speed index (m s^{-1})	7.3 ± 5.6	7.0 ± 3.2
Strike distance index (m)	179 ± 137	234 ± 94
Strike speed index (m s^{-1})	18.9 ± 9.4	19.5 ± 7.8
Wingbeat frequency index (beats s^{-1})	3.59 ± 0.6	3.17 ± 0.64

Table 2.26 Flight times and distance along with flight performance parameters for horizontal flapping flight (a-e) and gliding flight (f-k) of male and female Lanner falcons (*F. b. biarmicus* sp.). (a) the air speed at which power output for flights is least, (b) the air speed at which the ratio of power to speed is lowest, (c) lift:drag ratio at maximum range speed, (d) grams of fat consumed per kilometre at maximum range speed, (e) the minimum power required to fly divided by an estimate of the basal metabolic rate, (f) the minimum air speed required to avoid stalling, (g) the best achievable ratio of forward to downward movement, (h) the air speed at which the ratio of power to speed is lowest, (i) the lowest rate of descent attainable, (j) the minimum radius of a thermal in which the bird is able to climb, (k) the ground speed of cross-country flights (Jenkins 1995).

1995). In fact, with its high lift:drag ratio it can stay in the air with the aid of static or slope soaring gliding flights (Figure 2.34; Jenkins 1995). Most importantly this ability means that Lanner falcons are able to circle in small and large thermals and fly for longer periods, over greater distances, and to spend more time foraging from the air (Figure 2.35; Jenkins 1995). Ultimately, these abilities do not allow for very fast flights but they do allow Lanner falcons reduce fuel consumption and increase prey search time (Jenkins 1995). As consequence, breeding pairs very often occupy areas of low relief where thermals are used as the primary sources of lift for cross-

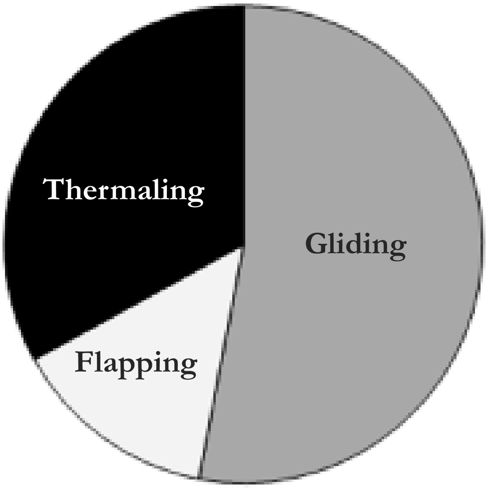


Figure 2.35 Flight activities averaged 53% gliding, 33% thermal soaring and only 14% flapping (Jenkins 1995).

country flying (see also *Slopes*; Jenkins 1995).

During very hot days both the male and the female birds have been observed to soar very high above the nest site for more than two hours at a time (Stephenson 2001). Nevertheless, temperature did not seem to significantly influence the flight behaviour of the Lanner falcon in either South Africa or Sicily (Jenkins 1995, Amato 2004). Langford (1912) thought that with their light bodies and weak plumage these falcons could not fly well in high winds. Mebs (1959), however, mentioned the importance use of cliffs with favourable winds for hunting in *F. b. feldeggii* sp. One study found that on windy days the female would sit on the cliff, after the chicks had been fed, while the male would cruise along a hill nearby, without hunting, for an hour or more (Stephenson 2001).

Despite these opposing point of views, Jenkins (1995) did not find any clear correlations between flight styles and wind speeds (calm/light wind and moderate/strong wind). Recently, a quantitative analysis in a sample area in Sicily has shown that during strong winds from north-east and south-east, Lanner falcons preferred to fly towards north, east and south (Amato 2004). Also, males seem to be more affected by unfavourable wind conditions than females, and tended to concentrate their hunting flights mainly to the less windy south and south-east directions (Amato 2004). During food provisioning to chicks at the nest, the flight times of males on windy days increased significantly with brood size and, interestingly, with a higher number of male chicks (Amato 2004).

The Lanner falcon has a relatively low wing loading (45.6 N m^{-2}) when compared to other bird-catching falcons such as the African Peregrine (60.25 N m^{-2}; Mendelsohn *et al.* 1989, Jenkins 1998). Lower wing loading enables Lanner falcons to soar well and it was these hunts from a soar that were commonly observed during a radio tracking study (Stephenson 2001). The wing shape of Lanner falcons also facilitates slower flight when coursing low over the ground searching for prey such as grasshoppers. This enables the species to make use of several different types of hunting method, and they are therefore more versatile than African Peregrines in their hunting ability (Stephenson 2001).

2.7 Voice

In birds, the syrinx is a structure analogous to voice box of humans, located low on the trachea and/or on the bronchi. Sound is produced either through vibration of the labia or the medial tympanum, or some combination of the two. It is modulated by cartilaginous rings in the tracheae, by C-shaped cartilages in the bronchi, or by both. In *F. b. feldeggii* the membrane is incomplete and in *F. b. biarmicus* the bronchidesmus is quite complete (Beddard 1903).

As outlined in Table 2.27, distinctions between calls are based exclusively on the behavioural context rather than on spectral and temporal features. Only a few basic vocalisations have been identified in all intra- or interspecific interactions (Bonora and Chiavetta 1975, Wrege and Cade 1977, Hatzofe 1995). In fact in vocalisations, falcons use mainly '*wailing*' and '*creaking*' (Leonardi *et al.* 2013).

Call sound	Tone	Behaviour and context
Kak-kak-kak	Harsh	Alarm, contact and soliciting
Kireee-kireee	Piercing	Alarm, exciting during food provisioning
Hek-hek-hek	Rasping	Anxiety near the nest
Kek-kek-kek	Clucking	Incubating or during food provisioning
Kyurr-kyurr	Trilling	Young soliciting food from parents
Ueeh	Plaintive	Young soliciting or during courtship
Chuk-chuck	-	During copulation
Kweep	-	Made after a piercing scream
Mciek	Sucking	When a partner is flying near the nest
Ko!	Guttural	During food provisioning or defense
Kre-kre-kre	Piercing	During food provisioning or defense
Teo-teo-treh	Keening	During copulation
Rih-rih-rih	-	When detect an intruder
Queck	Metallic	After the dispersion of young
Treeoo	Guttural	After the dispersion of young
Chup-chup	-	During bat-hunting

TABLE 2.27 The vocal repertoire of the Lanner falcon broken down by the behavioural context where it is performed. The transliteration of sounds is quite different and is dependant on the source literature (Bonora and Chiavetta 1975, Brown *et al.* 1982, Steyn 1983, Thomsett 1987).

Age	Vocalization	Behaviour and context
0	Peeping	Within the egg
3	Low cheeping	Comfort activity more strident when begging for food
5	Loud squark	When handled
8	Low '*kik*' cries	Hungry and excited at seeing food
11	Hissing	When suddenly disturbed
12	Low chittering	When handled, increasing as handiling continues
28	Deep '*kek*' notes	When catching sight of someone some distance away
38	Plaintive peeping	When handled
52	Soliciting call	Once feather growth was complete

Table 2.28 List of vocalizations made by a Lanner falcon chick at different ages. Data collected in captivity by Kemp (1975).

The repertoire of calls includes those uttered during courtship behaviour and for pair bonding, alarm calls in defence from intruders, and communication with young (Bonora and Chiavetta 1975; Table 2.27). Whitaker (1905) wrote about vocalizations: '*the note of this species is a shrill cry or shriek and the monosyllable 'cri' repeated two or three times expressed its alarm cry very well*'. MacLean (1984) summarized three typical calls: a harsh *kak-kak-kak*, a piercing *kirree-kirree* and a trilling *kirrr-kirrr*. Territorial calls in the Bamenda Highlands of Cameroon are most often audible around November to December (Sedláček *et al.* 2007). Sharpe (1904) heard and described alarm calls against dangerous intruders: '*when hovering over an owl make a great noise, especially just after their swoop*'.

During copulation, the male performed a '*chip chip*' or '*chuck chuk*' and the female a whine according to Snelling (1973). Brown *et al.* (1982) reported a sharp rasping '*hek-hek-hek-hek*' when anxious near the nest but also clucking calls by the incubating female on seeing the male with food. Parents in Tuscany, Italy vocalized during food pass before feeding chicks at nest (Figure 2.37; Morimando *et al.* 1997). The female made a loud and repeated '*chup*' for the chicks to feed at intervals of every two to three seconds (Stephenson 2001). Mebs (1959) noted that the Lanner falcon is almost silent outside the breeding season when compared with the Peregrine (Bonora and Chiavetta 1975, Brown *et al.* 1982, Leonardi 2001). A quantitative analysis of vocalisations confirms this tendency (Lanner = 0.4, Peregrine = 1.5 as relative frequency per *h*) but pairs were not quite as silent or as shy as supposed in previous studies (Leonardi *et al.* 2013).

The development of vocalizations from hatching to the fledging state is listed in Table 2.28. Solicitation calls by fledged young toward parents in order to obtain food were recorded for at least forty days but subsequently declined and disappeared when they were able to successfully capture prey independently (Kemp 1975). Young birds would also use a trilling *kyurrrr-kyurrr* call when begging food (Barbour 1971).

Frequencies of calls of *F. b. feldeggii* sp. ranged from 1.35 ± 0.40 kHz to 6.60 ± 1.27 kHz with Δ frequency 4.85 ± 1.27 kHz. Creaking calls are shorter (Δ time 0.28 ± 0.11 s) and higher pitched (1.40 ± 0.42 to 6.94 ± 0.94 kHz) than wailing calls (Δ time 0.49 ± 0.29 s; frequency 1.28 ± 0.38 to 5.24 ± 0.87 kHz; Figure 2.38 A, B; Leonardi *et al.* 2013). Sonograms from North African *F. b. erlangeri* sp. (Chappuis in Cramp and Simmons 1980) differ in peak frequencies (7-8 kHz) from the *F. b. feldeggii* race (6-7 kHz) probably due to the habitat preferences of these subspecies (Leonardi *et al.* 2013). In common with other species inhabiting open habitats, pairs of Sicilian Lanner falcons produce relatively short vocalisations (Δ time 0.37 ± 0.23 s; range 0.3 ± 0.3) with high peak frequencies (6.94 ± 0.94 kHz; range 9.2 ± 3.3 kHz) (Leonardi *et al.* 2013).

Call frequencies do not seem to be related to time of day, but females seems to be more vociferous than males at all breeding stages with the exception of courtship (Leonardi *et al.* 2013). Females especially tend to utter wailing calls from perches or inside the nest whereas creaking calls were not confined to a particular sex (Leonardi *et al.* 2013). Field evidence also reveals that solicitation calls by females were positively associated with brood size and it was found that breeding pairs with particularly vociferous males tend to have broods that contain more male offspring (Leonardi *et al.* 2013). Thus, vocalisations can be interpreted as honest signals in terms of indicating the genetic quality of Lanner falcon males which have better reproductive performance, both in terms of brood size but also in terms of the number of fledged young (Leonardi *et al.* 2013).

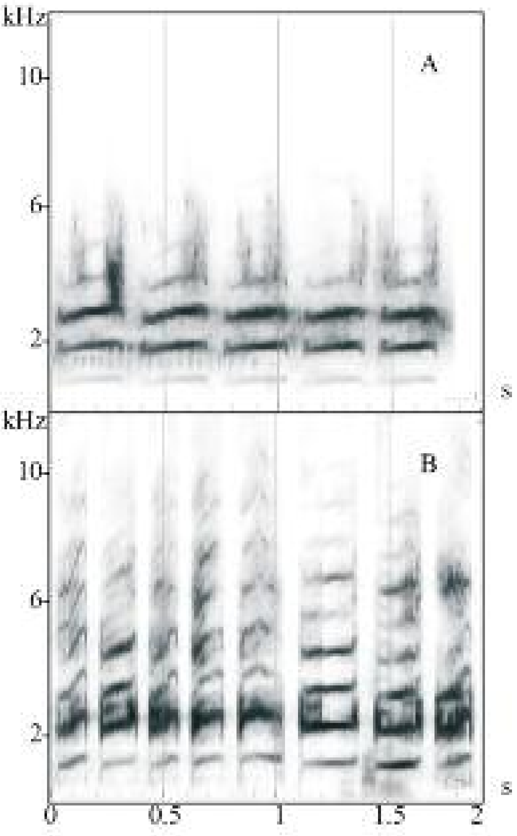


FIGURE 2.36 Examples of wailing (A) and creaking (B) calls uttered by the Lanner falcon (*F. b. feldeggii*) during the breeding season in eastern Sicily (Leonardi *et al.* 2013).

2.8 Longevity

Data on longevity are very scarce but the Lanner falcon has been known to survive in captivity for up to eighteen to twenty years (Bree 1859). The longevity record for a wild Lanner falcon is seventeen years (or more precisely 205 months; Mundy and Hartley 2002). This bird was starving and showed a protruding keel and a wound on the left wing (Mundy and Hartley 2002). Mirabelli (1982) gives a description of older individuals, observed in the hand in Calabria, southern Italy. These birds showed abnormal moult, pale feathers on the back and protruding bills (see also the section on *Moult*). In addition, he noted partial prey consumption by these individuals and in one case observed a presumed breeding failure due to an older male (Mirabelli 1982). Finally, in older females (*F. b. feldeggii*) feathers on the upperparts seem to tend to change from bluish to brown as in immature birds (Mirabelli 1982). This may be because, as senescence is a process in which endogenous oxidative stress increases with age, the synthesis of pheomelanin is affected accordingly (Galván and Jorge 2015).

FIGURE 2.37 A female Lanner falcon (*F. b. feldeggii*) vocalize after food pass, Eastern Sicily. © and courtesy of Markus Varesvuo.

Chapter 3.
Distribution and population estimates

3.1 Introduction

The current distribution of plants and animals is determined by the interaction between historical (paleogeographical and paleoecological) causes, inter-specific relationships, and the environmental needs of individual species (Huntley 1999). The Lanner falcon has a wide geographical distribution and so different environmental conditions could greatly affect its local abundance, leading to a process of fragmentation inside breeding populations (Leonardi 2001, Andreotti *et al.* 2008). Thus from south to north, previous Authors have distinguished between a wide and consistent sub-Saharan population and the more fragmented and ephemeral Palearctic populations (Cramp and Simmons 1980, Brown *et al.* 1982). The main argument proposed in support of this distinction was the afrotropical origin of the species, which meant it was less well adapted to harsher and colder climactic conditions (see Leonardi *et al.* 1992 for a review).

Unfortunately, the abundance and distribution of the Lanner falcon remains un-

Figure 3.1 A nest of the Lanner falcon (*F. b. erlangeri*) in the Roman aqueduct of Ras Mohammedia, Tunisia; © and courtesy of Hichem Azafzaf.

certain in many regions both in the Palearctic (i.e. Turkey) and in the Afrotropics (West Africa). Leonardi *et al.* (1992) and Leonardi (2001) provide comprehensive reviews of the status and distribution of the Lanner falcon by assembling evidence from numerous scattered observations. Nevertheless, a global and synthetic approach is necessary in order to identify which factors and drivers influenced population changes during the colonization process. The main aim was to construct a framework where data and inferences from various sources including genetics (*cf.* Figure 1.12), fossils (*cf.* Figure 1.3), morphology (*cf.* 2.26), and distribution (this chapter) could be combined to contribute to a better understanding of the current status. Thus, section 3.2 is a review of all the data available from literature sources and section 3.3 an interpretation of the results from the predictive model.

3.2 Historical biogeography

The recent genetic analysis of the Hierofalco complex shows a rapid diversification process with well-defined species (Gyr- and the Saker falcons) but also producing less pronounced differences at subspecies level (*cf. Phylogenetic relationships among subspecies*). In addition, hybridization events in contact zones seem to play a fundamental role in the current distribution and genetic diversity of the complex (Nittinger *et al.* 2005, 2007). An analysis of the inter-continental movements and phylogeographic structure of the Lanner falcon requires an understanding of its environment needs as well as the dispersal process which can be influenced by factors such as changes in migratory corridors and physical barriers such as deserts.

Based on these genetic studies it is possible to attempt a reconstruction of the colonization process at a large spatial level (Figures 3.2 and 3.3). During warmer periods of the Pleistocene three independent colonizations of Eurasia occurred (corresponding to three genetic clusters) and in the course of subsequent colder climactic periods the three Hierofalcon species remained isolated in refuge areas (Nittinger *et al.* 2005). Following the study made by Nittinger *et al.* (2005), using Neighbour-Joining (NJ) tree and maximum parsimony network of control region (CR) techniques, the first north-south split occurred between *F. b. biarmicus* and *F. b. feldeggii* (corresponding to the two main haploclades A and B; see Figure 1.12). *F. b. biarmicus* reached East Africa (Uganda) and an east-west split also occurred with *F. b. feldeggii* (that reached as far as southern and central Italy) directly linked with *F. b. erlangeri* of Morocco and *F. jugger* of the Indian continent (Figure 3.2). Nittinger *et al.* (2005) indentified three main haplotypes where the first (I) included only *F. b. biarmicus* individuals, thus supporting a Southern African origin for all of the races (Figure 3.2). In fact, *F. b. biarmicus* is the sole race that should be included in A (Mediterranean) and B (Afrotropical) haploclades (Figure 1.12). Considering the Lanner falcon as a unique species ($n = 6255$), the predictive distributional model map confirms a wide

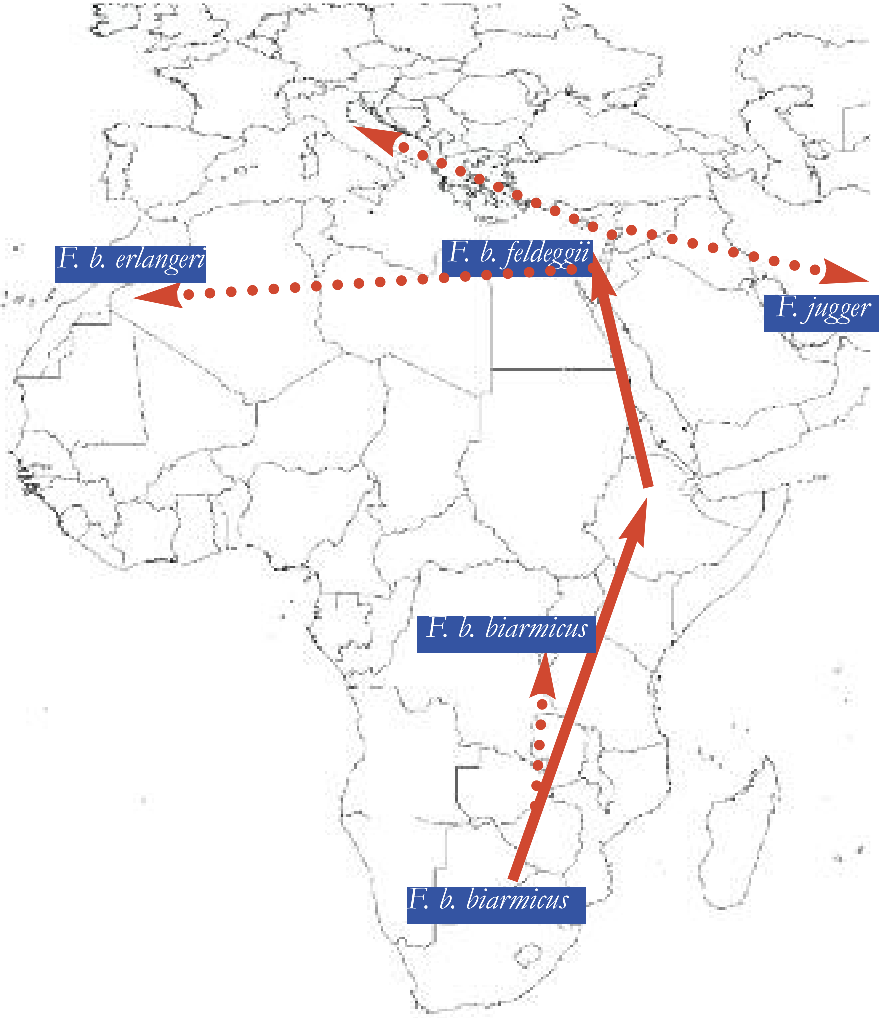


FIGURE 3.2 Possible pathways for the first colonization from Southern Africa.

core area in Southern Africa and a clear favourable pathway along the African Rift Valley (Figure s31). In the Palearctic, small suitable zones for colonization can be found in Israel, along the border between Syria and Turkey, in the Atlas Mountains in Morocco, and in the Tripoli province of Libya (Figure s31).

The second phase of colonization involved large contact zones with Gyr- and Saker falcons in the north of the Sahara and with the Saker only in the south. This scenario predicts a very large distributional area of the Saker falcon (Nittinger *et al.* 2007). In fact, the haplotype II includes individuals from Eastern Asia (Mongolia, Kazakistan) and central Europe (Austria, Slovakia) together with *F. b. biarmicus* of South Africa (Nittinger *et al.* 2005). *F. b abyssinicus* from Ethiopia derived directly from this halpotype and then moved towards western Africa (Cameroon). Another very large contact zone in Mediterranean Europe included Gyr- (Scandinavia), Saker (Mongolia), Laggar (India) falcons and the *F. b. feldeggii* population that previously reached southern and central Italy. From this haplotype III derived *F. b. tanypterus* and the Sicilian population of *F. b. feldeggii* (for the latter race see *Population densities in small and large islands*).

Morphological data (wing, tail and tarsus lengths) should be interpreted in the light of genetics (Figure 2.26 A, B). In fact, the NJ (Neighbour-Joining) tree regarding Lanner falcon females clearly shows two branches which fits well with the history of the races mentioned above with *F. b. erlangeri* splitting early from the other races (Figure 2.26 B). In addition the cluster with *F. b. tanypterus* and *F. b. feldeggii* is also reflected in the evidence for body features (Figure 2.26 B). The main tree branches for males are also in agreement with the genetics evidence but *F. b. erlangeri* males were only clustered with those of *F. b. biarmicus* (Figure 2.26 A).

Several intra-specific radiations appear to have occurred within the past 200–300,000 years, corresponding to the last two or three major Pleistocene glaciations (Guillaumet *et al.* 2008). During the Last Glacial Maximum (LGM) period, the Lanner falcon probably occupied the more suitable areas of the south western refugia (Figure s21, Ray and Adams 2001, López-López *et al.* 2008). These areas of southern Italy, Sicily, the southern Balkans, and coastal Turkey were covered by a predominantly grassland landscape with an overall 5-20% of tree cover, often occurring in patches (Figure s22 A; Ray and Adams 2001). In the north, the vegetation turned to a harsh steppe-tundra that represented the main distribution pathway for large falcons allowing the differentiation between the Gyrfalcon and the Saker falcon (*c.f.* 1.2 and Figure 1.3). Most probably, the colonization of Northern Italy and coastal northern Balkans began after the retreat of the ice-sheet (Figure s22 A). For this reason, Lanner falcons from Italy do not reach as far as France or Spain due to barrier formed by the Pyrenees covered by a perennial ice-sheet (Figure s22 A). This environmental limit is also evident in the Balkans where Greece represents the northern border (Figure s22 A). In this manner, colonization of Iberia would be possible only through the Straits of Gibraltar by the *F. b. erlangeri* race (mainly through wandering *juveniles*; Figure s22 A). However, the climate was probably too severe for this race and in fact fossil remains found in southern Spain belong to the Saker falcon (Marco 2004). This possible scenario for the Lanner falcon seems to be similar for a number of European raptor and owl species structured in meta-communities delimited by the suture zones of Eastern and Western refugia (i.e. Pyrenean and Balkanic suture zones; Figure s21; López-López *et al.* 2008).

Thus, climate change appears to be the main factor responsible for the fragmentation of the species range, and the adaptation to local ecological conditions in different refugia may also have acted to accelerate the speciation process (Guillaumet

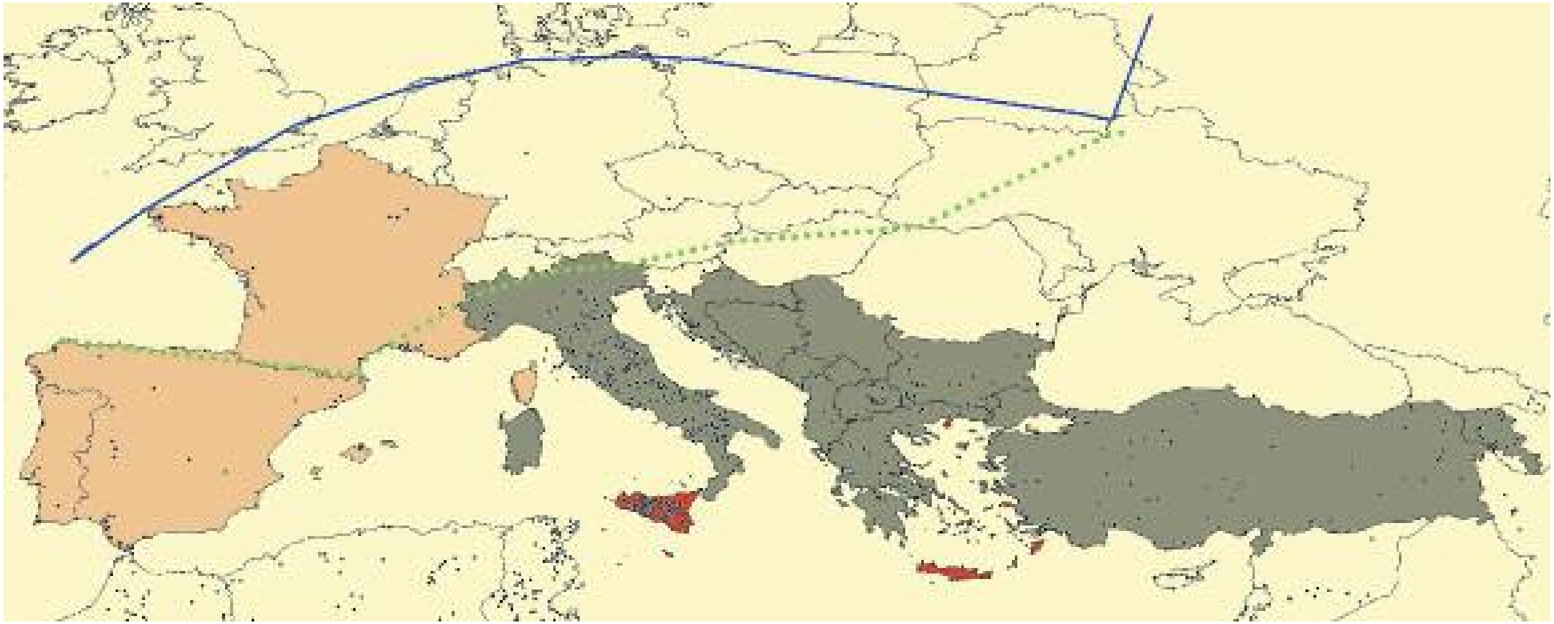


Figure s21 Southwestern (orange) and southeastern (grey) refugia for the European raptor community during the LGM (Last Glacial Maximum). The blue line indicate the maximum extent of ice sheet and the green dot line the maximum extent of permafrost. In red colour small and large islands where the Lanner falcon was recorded as breeding species for a period of at least 10 continuous years (see *Population densities in small and large islands*).

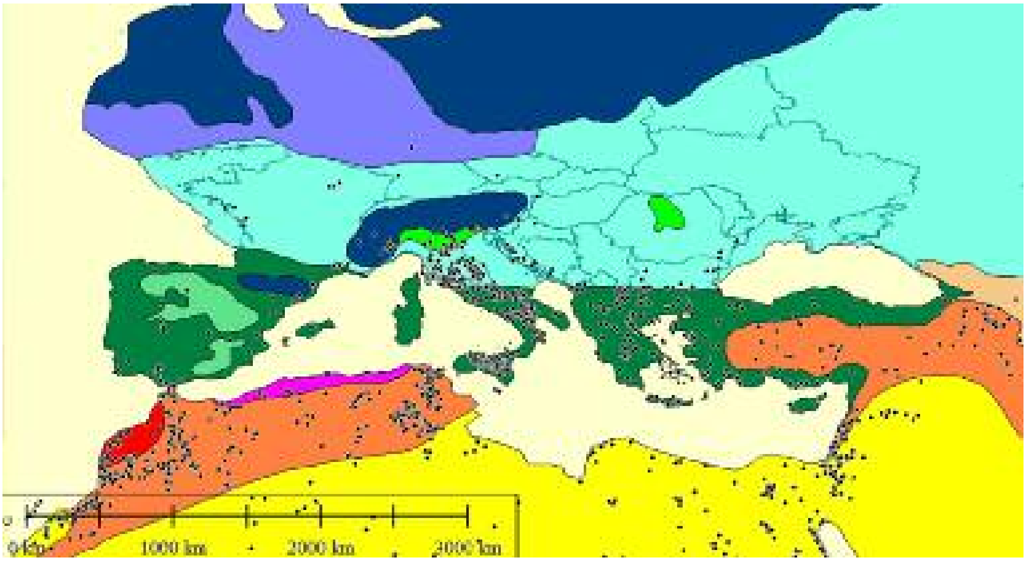


FIGURE s22 A Palearctic and Asia LGM (Last Glacial Maximum) vegetation map and spatial patterns of Lanner falcon sightings.

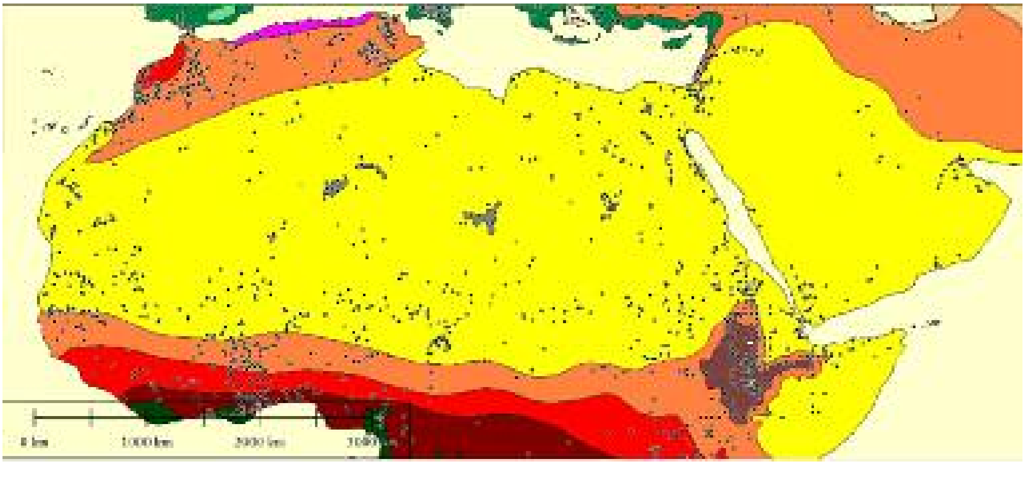


FIGURE s22 B Africa and Middle East LGM (Last Glacial Maximum) vegetation map and spatial patterns of Lanner falcon sightings. Tropical semi-desert and tropical grasslands currently occupied by F. b. abyssinicus were compressed. Tropical thorn scrub and scrub woodlands characterized the densely occupied Ethiopian region.

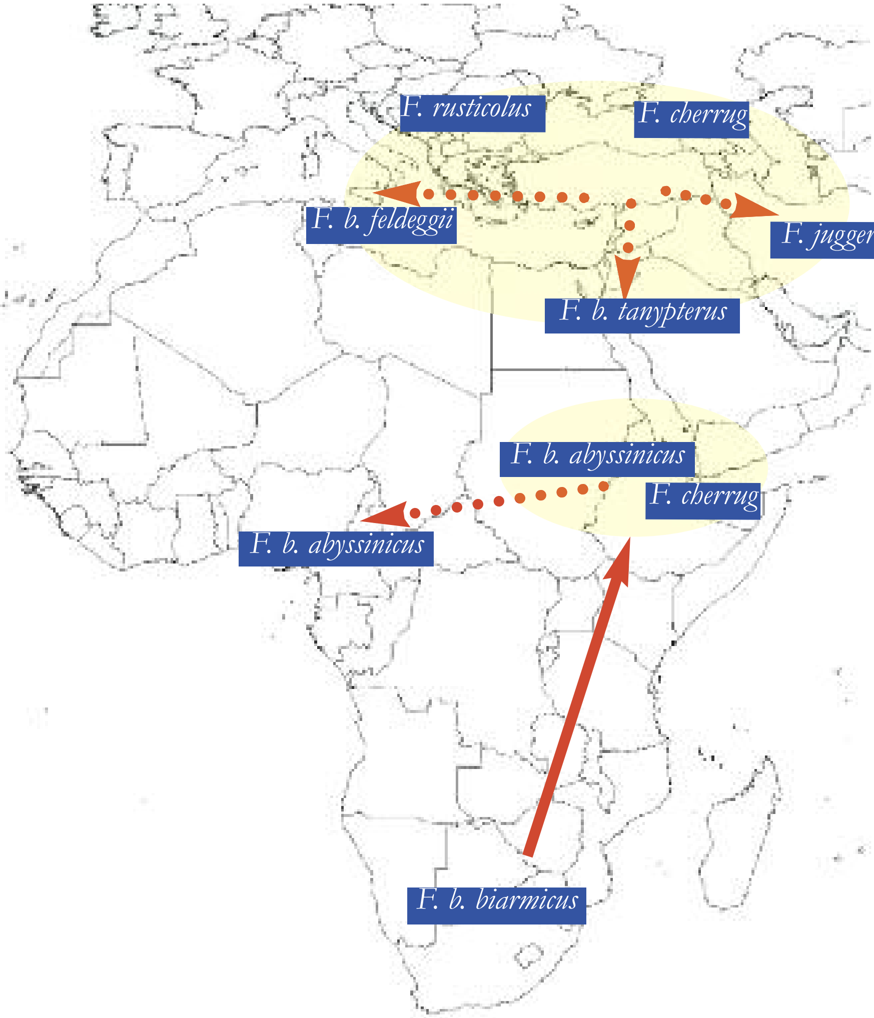


FIGURE 3.3 The second phase of colonization involved large contact zones between Lanner falcons and Gyrfalcon and Saker falcon populations in the north of the Sahara, and with the Saker falcon only in the south.

et al. 2008). It is probable that the first colonization started from sub-Saharan Africa but that the subsequent expansion of the Sahara, promoted north-south vicariance events and it is further possible that Plio-Pleistocene climatic fluctuations were responsible for additional east-west (for example between sub-Saharan Africa and India) vicariance events (Guillaumet *et al.* 2008, Korrida and Schweizer 2013). In this way, *F. b. feldeggii* from the Italian mainland is the only race directly connected with *F. b. biarmicus* A haploclade and Saker individuals, as well as Laggar falcons (see page 42 and Figures 1.12, 3.2 and 3.3). In the course of glacial temperature oscillations the southern boundary of the Sahara desert shifted further to the south (Le

Houérou 1992). Under these conditions the northern populations became more isolated and probably inhabited mainly the Mediterranean area (Figure s22 B). As a consequence, *F. b. erlangeri*, faced with this increase in unsuitable habitat, adapted by a component of its population exhibiting a partial seasonal migratory behaviour towards previously occupied areas in the eastern Sahara desert and in south-eastern Saharan Africa (Mauritania, Mali, and Chad; see Chapter 8).

It should be possible to ascertain which environmental conditions, driven by climatic change, promoted this isolation following the formation of the Saharo-Arabian belt in the Late Pliocene (Le Houérou 1992). During the intense and stable arid period (2-1 Ma) several periods of significantly increased precipitation have been identified. Thus, during these '*wet episodes*' the Saharan barrier was latitudinally compressed in relation to the maximum extent of aridity, and the east-west expansion of forests in equatorial sub-Saharan occurred as well as a north-south expansion of savannahs along the northern and southern forest edges (Figure s23). The re-establishment of arid conditions resulted in the contraction of equatorial forests, the development of natural barriers, and the disappearance of the ecological corridors that had allowed for jump dispersals to take place in the previous phase.

An in-depth analysis of the spatial distribution patterns of the Lanner falcon as a unique species revealed a number of '*hot spots*' of favourable environmental conditions for the species. It is possible to assume that (1) the stronghold of the Lanner falcon population is in Southern Africa, (2) the Rift valley of Eastern Africa represents a favourable pathway towards the Middle East and the wider Palearctic region, (3) the border between the Sahara desert and tropical West Africa represents something of a belt favourable habitat (but less so than the Rift Valley), (4) large regions of Morocco (such as the Atlas mountains) and Tripolitania in Libya represent favourable zones in North Africa, (5) few suitable zones are found in the Middle East (with some exceptions in Israel, Yemen, along the Turkish border with Syria, and some parts of Southern Iran), (6) no "hot spots" are present in Mediterranean Europe (Figure s24).

Overall, the predictive map lends supports to the theory that the origins of differentiation between the race of Lanner falcons began in Southern Africa where nominate *F. b. biarmicus* belonging to both haploclades is found. As for other subspecies, periodic expansion and contraction of the Sahara appears to have played a major role in clado-genesis (Guillaumet *et al.* 2008). Finally, the area of the Rift valley should split the populations of Lanner falcons of the highland steppes (*F. b. abyssinicus*) from those of xeric grasslands (*F. b. biarmicus*; Figure s22 B).

3.3 Distribution and abundances

As suggested from the historical biogeography data, the status and abundance of

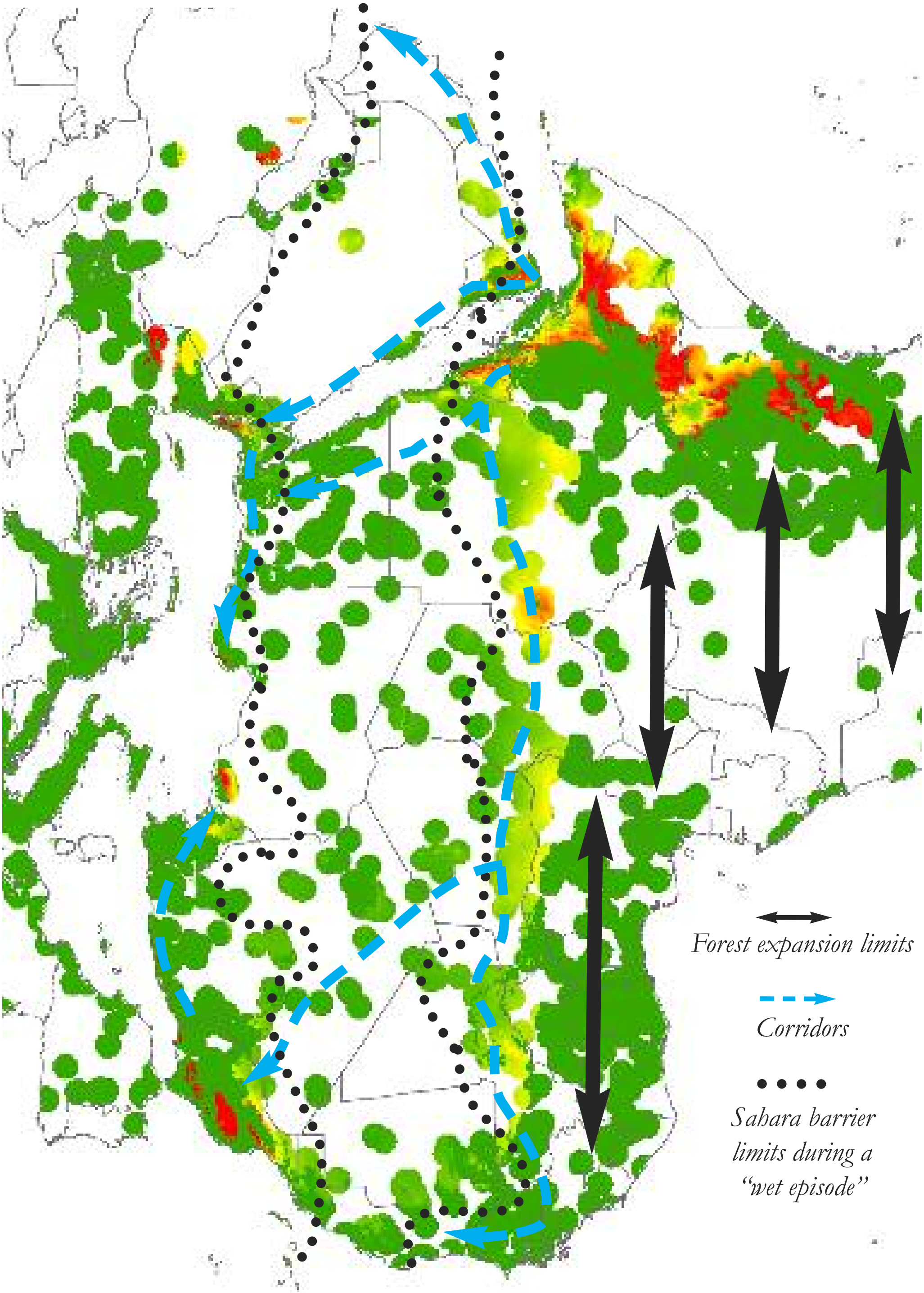


Figure s23 A simplified model of the expansion of the Lanner falcon ancestor during a '*wet episode*' in the Late Pliocene with the Saharan barrier latitudinally compressed.

Lanner falcon populations throughout the distributional area should be considered as a meta-population derived from a sink-source process (Leonardi 2001). Thus, where the Lanner falcon is a rare and localised species, in Mediterranean Europe for example, many attempts have been made to quantify the population, whereas it is very difficult to arrive at a reliable estimation of the number of breeding pairs in the Afrotropical zone. Table 3.1 shows the measured and potential population sizes of the Lanner falcon in different parts of its distributional area. It is problematic to make direct comparisons between these figures due to differences in methodology, study periods, accuracy, and field effort (Table 3.1). Nevertheless, such rough estimates should be of use in ascertaining vulnerability to many of the limiting factors which threaten populations, including anthropogenic pressures (Leonardi 2001).

Falco biarmicus feldeggii

Mediterranean Europe is occupied only by the *F. b. feldeggii* race (Fig. s25). The estimation of populations of this race is problematic due to its scarcity and consequent lower likelihood of detection in the field both in the past (*cf.* 1.2) and in more recent times (Leonardi 2001). Whitaker (1905) found it to be present in some parts of Italy, Dalmatia, Herzegovina, Montenegro, and Bulgaria. For Salvadori (1887) it is a localized species in Latium, Sicily, and around the Mediterranean. Until the 1970s very scarce information was available for the Lanner falcon including the identification of the northern distributional limit, an approximate knowledge of the spatial distribution of populations, and their vulnerability (Glutz *et al.* 1971, Bijleveld 1974, Bonora and Chiavetta 1975). For example in Sicily, Ciaccio *et al.* (1989) reported 20-30 bps before the 1980s, 60 bps measured in the 1980s, and an estimation of 60-100 more than the underestimated 100 and 50-200 bps for Italy and Mediterranean Europe respectively.

Unfortunately, after more than forty years, estimates are again confounded due to poor field coverage, misidentification with other large falcons, and the absence of long-term studies on breeding populations including survival and recruitment

Table 3.1 Measured and potential population sizes of the Lanner falcon in different parts of the distributional area (Ledant *et al.* 1981, Mirabelli 1982, Salvo 1984, Tarboton and Allan 1984, Thomson 1984, Frumkin 1986, Bergier 1987, Yosef 1988, I. Sela in Getraide and Hatzofe 1990, Siracusa *et al.* 1991, Magrini and Armentano 1994, Battista *et al.* 1995, Sigismondi *et al.* 1995, Grubač 1996, Handrinos and Akriotis 1997, Barnes 1998, Azafzaf 1999, Gustin *et al.* 2002, H. Azafzaf in Leonardi 2001, Barreau and Bergier 2001, Radović *et al.* 2003, Giovacchini 2003, BirdLife International 2004, Puzović *et al.* 2004, Caldarella *et al.* 2005, De Lisio *et al.* 2006, Andreotti and Leonardi 2007, Iankov 2007, Andreotti *et al.* 2008, Scott 2008, De Sanctis *et al.* 2009, Grubač and Velevski 2010, Velevski *et al.* 2010, Kotrošan and Hatibović 2012, Abuladze 2013, Guezoul *et al.* 2013, BirdLife International 2015).

Subspecies	Countries	Study period	Measured	Est.
F. b. feldeggii	Macedonia	1980-1991	7	14
F. b. feldeggii	Macedonia	2002-2009	14	25-35
	Demir Kapija Gorge	2007		0-1
	Tikveš Region	2007		1-2
	Pčinja Petrošnica Kriva Reka Rivers	2009		3-4
	Osogovo Mountains	2007		2
	Topolka Babuna–Bregalnica Rivers	2009		3-4
	Gradsko - Rosoman - Negotino	2011		2-3
	Lake Mantovo/Kriva Lakavica River	2008		1
	Pelagonia	2005		1
	Mariovo	2006		1-2
F. b. feldeggii	Europe	90s and 00s	127	480-900
F. b. feldeggii (?)	Lake Urumiyeh, Iran	70s	ca. 5	3-5
F. b. biarmicus	formerly Transvaal, South Africa	1975-1981	127	1340
F. b. erlangeri	Haouz, Morocco	90s		15-20
F. b. feldeggii	Sicily	80s		60-70
F. b. tanypterus	Judean and Negev, Israel	1980-1985	9	25-30
F. b. feldeggii	Greece	80s-90s		20-40
F. b. feldeggii	Serbia and Montenegro	1990-2002		8-12
	Srednja Srbija			2-3
	Vojvodina			0
	Kosovo and Metohija			2-3
	Crna Gora			4-6
F. b. feldeggii	Herzegovina	1993		12
F. b. feldeggii	Georgia			1-2
F. b. biarmicus	IBAs of Lesotho		14 – 22	34 – 59
F. b. erlangeri	Tunisia	1975-1990		300-400
F. b. feldeggii	Calabria, Italy	70s	8	8
F. b. tanypterus	Israel	1986-1988		20
F. b. biarmicus	Zimbabwe	80s		>1000
F. b. feldeggii	Croatia	2000		5
F. b. feldeggii	Italy	1999		172-191
F. b. feldeggii	Croatia	1989		10-20
F. b. feldeggii	Serbia	1989		5-10
F. b. feldeggii	Greece	1989		38-53
F. b. feldeggii	Turkey	1998		100-150
F. b. feldeggii	Georgia, Arm, Azer	1998		5
F. b. feldeggii	All breeding range	1999		330-429
F. b. erlangeri	Morocco	1980s		1000
F. b. erlangeri	Tunisia	1999		350-400
F. b. tanypterus	Syria	1980s		50
F. b. feldeggii	Central Apennines	1990s	7	10

Subspecies	Countries	Study period	Measured	Est.
F. b. feldeggii	Bulgaria	2000-2005		2-3
F. b. feldeggii	Abruzzi, Italy	2000s		10-12
F. b. feldeggii	Macedonia	2000s		10 – 30
F. b. feldeggii	Alto Jonio (Calabria)	1990s 2000s		2
F. b. feldeggii	Pollino and Orsato Mts (Calabria)	1990s 2000s		2
F. b. feldeggii	Marchesato (Calabria)	1990s 2000s		3-6
F. b. feldeggii	Gargano (Apulia, Italy)	2000s	6	6-7
F. b. feldeggii	Herzegovina (Bosnia Herzegovina)	1993		12
F. b. feldeggii	Majella National Park			2-4
F. b. feldeggii	Molise	1992 – 1994	10	16
F. b. feldeggii	Roccalbegna (Tuscany)	2000 – 2003		1-2
F. b. erlangeri	Ouargla Oasis, Algeria	2008-2009		2
F. b. feldeggii	Turkey			300-600
F. b. feldeggii	Central Southern Sicily	1972 - 1984		12
F. b. erlangeri	Ouarsenis, Algeria	1950s		8
F. b. feldeggii	Apulia and Basilicata	1983 - 1992	16-20	20-27
	Gargano		6-7	
	NW Murge		2-4	
	SE Murge		2-4	
	Matera Province		4	
	Potenza Province		4	
	Sub Appennine Dauno		probable	
F. b. feldeggii	Molise	2000s	6	
F. b. tanypterus	Galilee, Israel	1970-1975	4	
F. b. feldeggii	Italy	2000s		140-172
	Emilia-Romagna			0-3
	Tuscany			11
	Marches			11
	Umbria			5-9
	Latium			5-6
	Abruzzi			6-8
	Molise			4-6
	Apulia			11-16
	Basilicata			10-13
	Campania			3-4
	Calabria			4-5
	Sicily			70-80

rates (Andreotti and Leonardi 2007). In addition, for some countries such as Albania and Turkey, it is not possible to make an estimation due to a persistent absence of any data (in the case of Albania) or the existence of only very sparse data (in the case of Turkey). In the nineteenth century, a possible breeding population was identified in southern France, where a suitable habitat zone was also identified by the predictive model (Figure s25; Gustin *et al.* 2002). Three main historical core areas were identified for the Lanner falcon: Italy, the Balkans, and Turkey. Scattered breeding pairs (and also several sightings) regarding also small and medium Mediterranean islands (mainly in Greece) and the Caucasus region (Donázar *et al.* 2005, Abuladze 2013). Grubac and Velevski (2010) reported a stable trend for *F. b. feldeggii* in Macedonia from a survey with 80% coverage of the country (Table 3.1). It was found to be very rare in Slovenia, where there have been only two recent records. Thirty pairs have been found in northern Greece, and there have been occasional sightings in the Dodecanese islands, and more recently the figure has been estimated at 38-53 breeding pairs for Greece (Table 3.1). A nest has also been recorded in the Rhodopes Mountains bordering Greece and Bulgaria. The race is a resident and breeding species in the Karaburum Peninsula in the extreme western end of Turkey (Erdem *et al.* 2002). In the past sixty years, in the whole of the Southern Caucasus (Armenia, Azerbaijan, Georgia), there have been 30 observations in Georgia with 1-2 pairs breeding sporadically (Abuladze 2013). In Georgia it has been extirpated as a regular breeding species, although it has been identified as an extremely rare year-round resident with local seasonal movements (Abuladze 2013). It is resident in Bosnia-Herzegovina but present as a regular breeder only locally in Herzegovina. Estimations of population size have not been made, but there are probably only a small number of pairs (Kotrošan and Hatibović 2012). Resident in Eskişehir, Turkey and Ercek Lake, Van, Turkey (1-4 individuals; Özelmas and Karakaya 2011).

Falco biarmicus erlangeri

The North West African race, *F. b. erlangeri* inhabits Morocco, Western Sahara, Mauritania, Tunisia, Algeria, and Western Libya (Leonardi *et al.* 1992). At the beginning of the twentieth century it was considered abundant in Algeria, Morocco, Tripoli, and Cyrenaica regions, as well as sparingly in Spain (Whitaker 1905). It is resident in these regions and is the commonest large falcon in Tunisia particularly in the south and less so in the north (Whitaker 1905). It is the breeding sub-species at Banc d'Arguin, Mauritania (Bijlsma 1990). It is common in Tripolitania and Fezzan occurring in many places but with large gaps in the breeding distribution (eastern Libya; Erard 1970). It is also the most common large falcon in Morocco (Irby 1895). It was found to be resident and breeding in the Ouargla Oasis, Algeria (Guezoul *et al.* 2013) as well as breeding in Saharan Morocco (Bergier *et al.* 2010) and has been identified as resident breeding species and a possible Palearctic migrant in Morocco (Bergier and Thevenot 2010). It is commonly found on high plateaus, along the Saharan border, and in suitable desert regions, although it is rare or absent in the Tell (1970s; Ledant *et al.* 1981).

It has been found to be fairly common in Haggar and Tassili, Algeria (1960s) (Ledant *et al.* 1981) and common and widespread in Egypt, especially at Fajum (Antinori 1864). Resident in Tagat and Arar in Mauritania (Gee 1984).

Falco biarmicus tanypterus

Tristam (1865) considered the Lanner falcon fairly common among large falcons and distributed throughout Israel from Elat in the south to the Samarian desert in the North (Yosef 1988). In Israel it is a widespread rare resident in the Eastern Shomron, Judean and Negev deserts (Shirihai *et al.* 2000). Similarly in Egypt, it is the most abundant large falcon (Cavendish Taylor 1859, Shelley 1871). Fairly frequent in Sudan from Ad Douiem southwards and most common in the White (Sudan) and Blue (Ethiopia) Nile regions (Butler 1905).

In Lebanon, is a Palearctic migrant, a winter visitor and an uncommon summer breeder (Ramadan-Jaradi and Ramadan-Jaradi 1999), breeding in the Jordan Valley and the Negev (1930s). Rare resident in the Rum desert avifaunal region and Mudawwara desert avifaunal region, Jordan (Evans *et al* 2005). In North Yemen (1970s-1980s), it was common and widespread (Philips 1982). In Syria during the 1960s, nesting was widespread throughout the country, and it was recorded as occasional visitor to neighbouring countries, and bred in the border areas between Syria and Lebanon (Kumerloeve 1968). Resident and breeding in the Red Sea mountains and along the coastal plain of Egypt (1930s).

Falco biarmicus abyssinicus

In Somalia the species is fairly common and resident breeders are present throughout the year (Ash and Miskell 1998). In Ethiopia and Eritrea, it is also a widespread and common resident but in both countries there are large areas with few or none (Ash and Atkins 2009). Common and widespread in Adis Abeba area, Ethiopia (1940s) (Guichard 1950). For Salvadori (1884) the falcon is less common in Shoa (an historical region of Ethiopia).

In 1901 it was said to be common '*all the way from the coast to the Abyssinian highlands*' (Ogilvie-Grant and Reid 1901). In Eritrea, and particularly in the Zula bay area (Northern Red Sea), it was described as resident and common in the 1950s (Smith 1957). In Liberia (1990s), it was an uncommon dry season visitor into the North (Gatter 1997).

In Togo (1980s), it is not uncommon, presumed resident throughout, especially in northern the savanna (Cheke and Walsh 1996).

It is a resident but occasional breeder in the Central African Republic (1980s; Carroll 1988). Scholte *et al.* (1999) described it as a resident and common in the Waza-Logone area of northern Cameroon, visitor to Gambia during the dry season between November and May. Thiollay (1978) observed the Lanner falcon less frequently in Mali than in northern Cameroon and Chad. It has been frequently observed in Chad and Niger (1970s; Newby 1981).

In Mali it is a resident and a Palearctic migrant species (1970s) (Lamarche 1980). In Nigeria (1970s) it has been described as a scarce resident (Elgood 1982). It is less common in Senegal and Gambia, with scattered observations along the Niger borders, coast of Angola, and South Sudan (Rochebrune 1884).

Falco biarmicus biarmicus

It is distributed virtually throughout Southern Africa with a stronghold in Lesotho and south-eastern South Africa (Jenkins 1997). In South Africa, it is commonly encountered everywhere (1910s) (Finch-Davies 1920). Newman (1979) reports observations in southern Africa from the Cape and Drakensberg to the Kgalagadi Transfrontier Park.

It is only an occasional visitor in the Mountain Zebra National Park (Eastern Cape Province, South Africa) (Craig *et al.* 2005), a scarce resident in West Coast National Park (Western Cape province, South Africa), and a rare resident in Sehlabathebe National Park, Masite, and the Qeme Plateau, Lesotho (Kopij 2002, 2010). In Botswana (1980s and 1990s), sparse to common resident throughout and it is the most common large falcon in the country (Penry 1994).

In Angola, it is an uncommon resident, mainly found in the south of the country and in the central plateau (Dean 2000) and in Mozambique (1990s), it is described as an uncommon breeding resident (Parker 1999).

Mostly resident throughout Zambia (2000s; Dowsett *et al.* 2008). In Zambia (1960s), it occurs almost everywhere usually in sparse densities but is particularly scarce in the Northern province (Benson *et al.* 1971).

It is an uncommon or local resident with singles or pairs occasionally seen hunting in Nyika National Park (Malawi-Zambia) (Dowsett-Lemaire 2006). For Lewis and Pomeroy (1989), the Lanner falcon is uncommon and widely distributed south of 17°N apart from the equatorial lowland forest areas of the west, and Kenya seems to represent the eastern limit of the species range.

In the 1970s, it was said to be common in Karamoja (Uganda), to occur in northeast part of the Teso district (Uganda), and to be resident in small numbers in the Tsavo East National Park (Kenya) (Mann 1976, Lack *et al.* 1980).

Field surveys

Periodic surveys made by sampling transects of suitable habitat areas in Africa, especially the central eastern and southern countries (Table 3.2). In the formerly Transvaal region, encounters with the Lanner falcon varied between Highveld and flat, hilly bushveld areas (Tarboton and Allan 1984).

During an aerial survey along 250 km of the Ghaap Plateau escarpment (Northern Cape Province, South Africa) only one Lanner falcon was detected (Anderson and Hohne 2007). Lanner falcons tend to slip off their nesting ledge (usually an old

Subspecies	n/100 Km	Study area
F. b. biarmicus	0.08	Formerly Transvaal, South Africa
F. b. biarmicus	0.06-0.10	Kenya
F. b. abyssinicus	0.20	N Cameroon
	0.30	N'Djamena, (Chad)
	0.60	Lake Chad (Chad – N Cameroon)
F. b. erlangeri	0.06	Eastern Anti-Atlas Mts, Morocco
F. b. abyssinicus	0.80	Guinea
	1.40	Haute Guinée
	0.50	Guinée forestière
	0.20	Moyenne Guinée
	0.40	Guinée maritime
F. b. biarmicus	0.24	CS Namibia
F. b. biarmicus	0.14	CS Kenya (unprotected areas)
	0.17	S Kenya (protected areas)
F. b. biarmicus	0-4.30-8.60	Kalahari National Park, SA
F. b. abyssinicus	0.40	S Mauritania and N Mali (Sahel)
F. b. feldeggii	0.10	N Evros Delta
F. b. abyssinicus	0.05	Zakouma National Park (Chad)
	0.003	Manda National Park (Chad)
F. b. abyssinicus	0.10	Assop falls and Forest Hills Reserve (Nigeria)
F. b. biarmicus	0.10	Sehlabathebe Nat Park, Lesotho
F. b. biarmicus	0.08	Zimbabwe
F.b. abyssinicus	0.10	Boé region, SE Guinea-Bissau

Table 3.2 Field surveys made in several different countries. Road and aerial counts made mainly with regard to the afrotropical races (*F. b. abyssinicus* and *F. b. biarmicus*) (Bauer *et al.* 1969, Thiollay 1978, Vernon 1979, Tarboton and Allan 1984, Oliver 1987, Kopij 2002, Rondeau *et al.* 2007, Simmons and Barnard 2007, Anadon *et al.* 2010, Ogada *et al.* 2010, Ramos and Díaz-Portero 2013).

crows nest) and dive away below the helicopter, so they can easily be missed during surveys (Anderson and Hohne 2007).

Although significant environmental transformations have occurred, no significant change in densities of the Lanner falcon between years was found by Thiollay (2001) using road indexes (*F. b. abyssinicus*) in northern Cameroon between 1973 and 2000 (Table 3.3). In fact, only species of small raptor such as the Lanner falcon, which can adapt to human inhabited and cultivated areas, were found to show stable populations (Thiollay 2001).

Population densities in small and large islands

A large number of islands and islets are also used by breeding pairs of Lanner falcons or are reached by wandering individuals (Table 3.4). The Lanner falcon is frequently observed as being present or nesting in the western Mediterranean islands, which is in keeping with the refugia theory (Figure s21, Table 3.4). Conversely, sightings are much scarcer with regard to islands in the eastern Mediterranean (the Balearic islands for example) or Macaronesia (such as the Canary and Cape Verde islands) (Figure s21, Table 3.4). A recent review by Donázar *et al.* (2005), points out that the probability of presence on an island increases in proportion to island area and with proximity to a migration route. Thus, a partially migratory species such as the Lanner falcon is more prone to maintaining populations on islands than wholly migratory or sedentary species (Donázar *et al.* 2005). In this way, large islands located close to a nearby mainland are very suitable for colonisation, an example being Sicily which holds the largest Mediterranean population of the Lanner falcon (Figure s21, Table 3.4). In these cases, the water bodies may act as a semi-permeable barrier, creating a metapopulation structure for species such as the Lanner falcon that may result in lower probabilities of the colonization of appropriate habitats and lands beyond the barrier (Donázar *et al.* 2005).

1973	**2000**	**Road transects**
1.9	2.9	Garoua – Rhumsiki – Moloko
1.7	3.3	Moloko – Koza – Mora
1.0	1.0	Mora – Maroua – Lara – Yagoua
1.3	0.6	Yagoua – Pouss – Guirvidig
2.9	1.5	Mora – Waza
1.7	1.3	Waza National Park
15	**14**	

Table 3.3 Comparisons between road indexes from 1973 and 2000 from Thiollay (2001).

Subspecies	Location	Name	Status	Density
F. b. feldeggii	Crete, Greece	Dia (Δία)	R, Br	1 bp
F. b. feldeggii	Ionian Sea, Greece	Corfu (Κέρκυρα)	R, Br	?
F. b. feldeggii	Aegean Sea, Greece	Lesbos (Λέσβος)	R, Br ?	?
F. b. feldeggii	Aegean Sea, Greece	Kos (Κως)	R, Br	?
F. b. feldeggii	Ionian Sea, Greece	Cephallonia (Κεφαλλονιά)	Obs	-
F. b. feldeggii	Lake Urmia, Iran	Ashk (اشک)	SBr	1 bp
F. b. feldeggii	Lake Urmia, Iran	Arezu	SBr	2 bp
F. b. tanypterus	Yemen	Socotra (سُقُطْرَى)	Br?	2 bp
F. b. feldeggii?	Cyprus	Cyprus	Ac	<5 obs
F. b. tanypterus	Lebanon	Jazeerat an-Nakheel	M	1 ♀
F. b. feldeggii	France	Corsica	NR	-
F. b. erlangeri	Canary islands, Spain	Tenerife	Acc	<10 obs
F. b. feldeggii	Greece	Crete (Κρήτη)	R, Br?	>3 bps
F. b. feldeggii	Greece	Rhodes (Ρόδος)	R, Br?	1bp
F. b. feldeggii	Daltatia, Croatia	Pag	?	1 obs
F. b. erlangeri	Tunisia	Zembra	R, Br	1 bp
F. b. feldeggii?	Spain	Mallorca	Ac	-
F. b. feldeggii	Italy	Sicily	R, Br	60-80 bps
F. b. feldeggii	Aegean Sea, Greece	Thasos (Θάσος)	R, Br	-
F. b. feldeggii	Aegean Sea, Greece	Samos (Σάμος)	R, Br	-
F. b. feldeggii	Aegean Sea, Greece	Naxos (Νάξος)	R, Br	1 – 2 bps
F. b. feldeggii	Italy	Sardinia	Acc	<3 obs

TABLE 3.4 The status and abundances of the Lanner falcon on different islands and islets in the Palearctic and the Middle East (Dresser 1871-1881, Kirwan *et al.* 1996, Handrinos and Akriotis 1997, Thibault and Bonaccorsi 1999, Donazar *et al.* 2005, Clarke 2006, Andreotti and Leonardi 2007, Scott 2008, Ramadan-Jaradi *et al.* 2008, Dudley 2010).

Other small Greek islands host some breeding pairs that have probably suffered due to their isolation (Table 3.4). In fact, the birds found on Rhodes are probably not breeding as has been stated in the past (Handrinos and Akriotis 1997). Handrinos and Akriotis (1997) consider the Lanner falcon as a recent colonist of Crete with a definite breeding record from 1977, but nests were recorded previously by Dresser (1871-1881). Thus, as suggested by Donázar *et al.* (2005), the Lanner falcon populations in the Greek and Turkic archipelagos could be maintained by the existence of the species in an area of 500 km radius around the islands due to post-colonization through a '*rescue effect*'.

Individuals from Sicily are genetically different from those of northern and southern Italy and probably they were part of a subsequent colonization process when the species came into contact with Gyr- Saker and Laggar falcons (Nittinger *et al.* 2005; Figure 3.2). Crossings of large areas of open sea by the Lanner falcon (*F. b.*

feldeggii) are improbable based on recent recorded movements (see Leonardi *et al.* 1992, Leonardi 2001 for reviews). In fact, very few individuals (range 0-2 per year) were observed during seasonal movements in the Messina Strait or across the Adriatic sea (see Chapter 8). Unfortunately, there are no fossil records of the Lanner falcon in Italy but only Gyr- and Saker falcons in southern regions (Figure 1.3; Bedetti and Pavia 2007). In addition, individual Saker falcons from Hungary seem to regularly over-winter in Sicily where they shift their diet to insects and birds (Corso and Harris 2012, Bondì *et al.* 2014). Among Hierofalcons, *F. biarmicus*, *F. cherrug*, and *F. rusticolus* were found not to be monophyletic as a result of incomplete lineage sorting of ancestral polymorphism and/or recent hybridization (Nittinger *et al.* 2005, 2007, Fuchs *et al.* 2015).

The reconstruction of ancestral character states made by Fuchs *et al.* (2015) using the maximum likelihood algorithm for three eco-ethological characters (diet, migration, and habitat) shows an increasing migratory tendency from the Lanner falcon to Gyrfalcon passing through the Saker. This sedentary tendency of the Lanner falcon could possibly be linked to stable favourable habitat conditions but only in some limited zones during the Late Pleistocene (Pérez-Tris *et al.* 2004). In fact in southern Italy during glacial periods, open vegetation assemblages (i.e. *Chenopodiaceae*) were restricted to limited areas whereas at middle latitudes deciduous forests were dominant and, above all, temperatures were lower (Combourieu-Nebout *et al.* 2015). Thus, it is possible to hypothesize a small population of the Lanner falcon in Sicily, strongly limited by large wooded areas occupied by Gyr- and Saker falcons that, in turn, increased chances of hybridization (Nittinger *et al.* 2005). At the end of the LGM, Gyrfalcons moved towards the extreme north, and Sakers to the east, although they may have retained winter quarters in the original areas. The Lanner falcon in Sicily expanded across the newly-available favourable territory whereas the first mainland populations were limited both to the north and to the south. As a consequence: (1) the stable Sicilian population did not play a role as a source for the mainland Italian populations (or for the so-far small deme in Calabria), (2) the strangely '*inverted*' situation where the size of the island population exceeds that of the mainland becomes plausible, and (3) the absence of a migratory tendency in spite of a water body a mere 3.14 km wide (the Strait of Messina) also becomes plausible.

In Socotra, *F. b. tanypterus* (?) is possibly a resident breeder. Two pairs tentatively identified as Lanner falcon were recorded on Dimimi (in the Hagghier range) and in the Dimichiro valley in 1898-99 but it appears that definitive views were not obtained of either pair. Occurrence of this species on Socotra may therefore require confirmation (Kirwan *et al.* 1996).

In Iran, the Lanner falcon was first discovered in August 1971, breeding on islands in Lake Orumiyeh. At least five pairs were subsequently located, mostly on small islets. As it has only been observed in summer, it is perhaps only a summer visitor to the area (Scott 2008). This is the sole case reported of summer breeding by the Lanner falcon in the Northern Hemisphere. Nevertheless, in Inner Anatolia a nest has been found with one unhatched egg and three 10-day old chicks where eggs were presumably laid in the first week of April (Kirwan *et al.* 2008). Perhaps an effect of longitude could explain this discrepancy.

Sightings of Lanner falcons in the Canary Islands (all islands except La Palma and El Hierro) are especially prevalent in spring (between February and May) and appear to be accidental landfalls of birds moving elsewhere (Clarke 2006). There was one recorded sighting in 1971 in Menorca, as well as occasional sightings in winter, such as in 1957-1958, but these may be mis-identified Saker falcons (Flint and Stewart 1992).

Countries with uncertain status, distribution and population size

Dresser (1871-1881) considered the Lanner falcon a habitat generalist in Bulgaria with a smaller population than the Saker, but with a more widespread distribution (based on several scattered observations) although he could supply no further evidence from the past with regard to the status of the species in Macedonia (Dresser 1871-1881). The status of the species there remains uncertain (as it often confused with Saker and Eleonora's falcons), but it is probably a rare resident in very small numbers in all regions except Thrace and along the Black Sea coast (Beaman 1986). Nevertheless, many published records must be erroneous. Tristam (1865) reported at least five or six nests in Jericho (Wadi Qelt), near Wadi Hamam and Wadi Leimun (Gennesaret). In the former USSR, the only recorded nest was detected in 1949 in the Caucasus (Leonardi *et al.* 1992). In Lebanon, the species was formerly considered a possible breeder but there is no confirmatory evidence that this is the case (Ramadan-Jaradi *et al.* 2008). The species was apparently more common in Greece during nineteenth century and up until the 1950s (Handrinos and Akriotis 1997).

The Lanner falcon is considered rare in Serbia and Montenegro due to a very small population of only around eight to twelve breeding pairs (Puzović *et al.* 2004). It is also considered rare in Slovenia with only two recent observations (Hanžel and Šere 2012). It appears to be a regular breeder locally in Herzegovina, with the last estimation for 1993 being twelve breeding pairs. More recent estimates of population size have not been made, but there probably remains a small number of pairs. (Kotrošan and Hatibović 2012). Grubač and Velevski (2010) measured estimated a population of 4.5% as a percentage of the European population in Macedonia. The status in Albania remains completely unknown, and the species is said to be critically endangered in Croatia (Mazal and Mikulić 2012). Although first observed as a breeding species in 1933, the status and distribution in Turkey remain poorly understood largely due to confusion with other large species of falcon (Kirwan *et al.*

2008). It is a rare species in all regions, localized along the Black Sea coast and is absent in Thrace (Kirwan *et al.* 2008). In Bulgaria the species status is also considered to be critically endangered with separated isolated localities noted in Eastern Rhodopi, Rila, in the western frontier mountains (Iankov 2007). In Romania, there are insufficient confirmed records with regard to the Lanner falcon.

In Kuwait, *F. b. tanypterus* it has been extremely difficult to determine the exact number of reliable records of wild birds in a region where it is rare and to which is disperses in autumn, winter and spring (Gregory 2005). It is also a rare visitor to Iraq (Salim *et al.* 2012). In Oman (1970s), the status is uncertain, and, although it may be an occasional visitor, reports may well include escapes and misidentified Saker falcons. However, there are confirmed records from Lake Urmia (Ormiyeh), Iran where the population remains stable at at least five breading pairs (Eimanifar and Mohebbi 2007).

F. b. biarmicus is common from Lake Tanganyika to the Semliki Valley and might also occur in the north eastern Katanga province of the Democratic Republic of Congo (Petersen 2010). *F. b. abyssinicus* is fairly common, from Uele to the Sudan border, and probably also as far south as Lake Albert, although it is rare in the Equateur province (Petersen 2010).

Contact zones among subspecies

Across several zones of their distributional area different races of Lanner falcon can be found at the same time (Figure s25; Chapter 8). These contacts between races mainly concern *F. b. abyssinicus* and *F. b. erlangeri* (in the Sahel), *F. b. tanypterus* and *F. b. abyssinicus* (in South Sudan, Eritrea, Somalia) and *F. b. tanypterus* and *F. b. feldeggii* (in Turkey) (see Chapter 8). A number of reports and sightings confirm this scenario. At Bajil on the Tihama (North Yemen) on 12 March one adult and one *juvenile* were of the local race *F. b. abyssinicus* and one *juvenile* of the '*Levant*' race *F. b. tanypterus* (Cornwallis and Porter 1982). In this region, all adults identified to subspecies were *F. b. tanypterus* whose nearest breeding area is in northern Sudan. Its presence might therefore indicate a hitherto unknown extension of the breeding range for this species (Brooks *et al.* 1987). In this case it would certainly seem to be a passage migrant and winter visitor in small numbers, but also an uncommon breeding resident, with *juveniles* in a family party having been seen in June (Brooks *et al.* 1987). Heim de Balsac and Mayaud (1962) wrote: *'Où se situe la limite entre les races* erlangeri *et* abyssinicus*?'* They stated that birds in Tamanrasset (Algeria) are paler than those from other parts of Algeria and Tunisia, suggesting that birds from Ennedi (northern Chad) and Borkou (Chad) are *F. b. abyssinicus* and those observed in Banc d'Arguin (Mauritania) belong to *F. b. erlangeri*. Jany (1960) and others captured specimens belonging to *F. b. erlangeri* at Wadi el Fareigh (Western desert), in Djalo oasis Audjila and in Kufra Oasis (Cyrenaica, Libya). The Authors referred at different times to both *F. b. erlangeri* and *F. b. tanypterus*. In Sudan and South Sudan (1980s) *F. b. tanypterus* was considered fairly common while *F. b. abyssinicus* was thought to be uncommon (Nikolaus 1987).

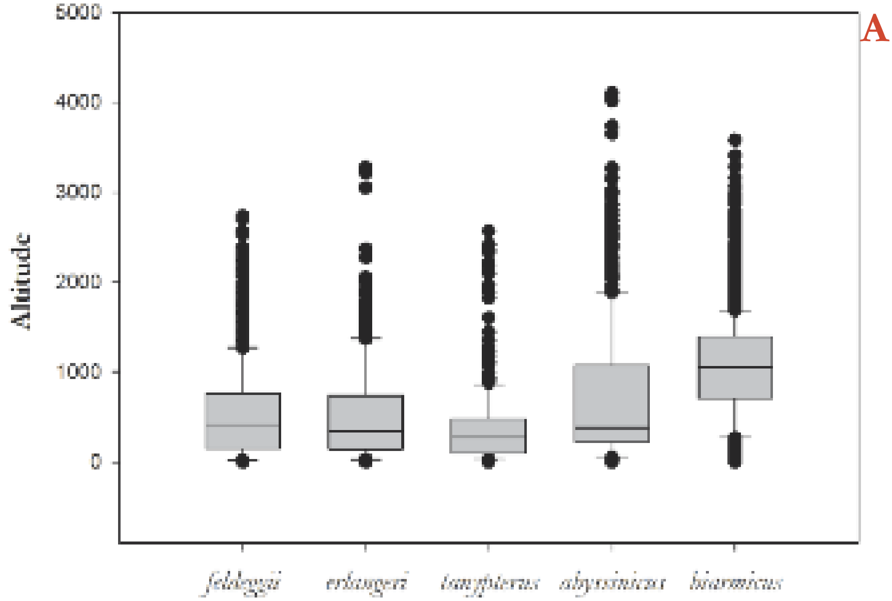
In East Africa two races are found: the resident *F. b. abyssinicus* (Eritrea, Ethiopia and North Somalia) and *F. b. tanypterus* (migrant from North Africa in Eritrea and North Ethiopia). The *F. b. abyssinicus* race ranges through North Kenya South to Lake Baringo (Kenyan Rift Valley) and more southern birds are nominate *F. b. biarmicus*. Breeding pairs of *F. b. erlangeri* found north of Kidal (northern Mali) and Nouakchott (Mauritania), occupy Sahara, Oued Edhahab (Western Sahara), Zemmour (Morocco), Banc d'Arguin (Mauritania), and perhaps the Tenere desert, as well as being occasionally found in Senegal during winter (Thiollay 1977). Seven old records exist relating to *F. b. tanypterus* sightings in Eritrea and North Ethiopia above 12°N (Ash and Atkins 2009). Other records from North Uganda might be referable to the race *F. b. abyssinicus* and in the south west the nominate race probably occurs (Carswell *et al.* 2005). Overall, the *F. b. abyssinicus* race ranges from south Uganda and the Great Lakes while *F. b. biarmicus* ranges from South Africa north to Kitui (Kenya; Sclater quoted in Friedman 1930).

3.4 Modelling[1]

A non-parametric Random Forest (RF) model was used to predict distribution patterns of the Lanner falcon because this type of model is known to be able to accommodate large numbers of input variables without overfitting (Biau 2012). Predictive distributional maps (Figure s24 and s25) are based on 6255 sightings of which 739 are of *F. b. feldeggii*, 630 of *F. b. erlangeri*, 534 of *F. b. tanypterus*, 1189 of *F. b. abyssinicus*, and 3163 of *F. b. biarmicus*. Four main independent environmental variables were used: altitude (metres above sea level), annual temperature (°C × 10), annual precipitation (mm), and seasonal precipitation (the Coefficient of Variation is the standard deviation of the monthly precipitation estimates; Figures 3.4-3.5).

[1] The data consist of sightings collected mainly from the scientific literature spanning a period of twenty-five years, from personal communications, from locations of photographs of the species, and from internet sources. The bulk of these data were collected during the preparation of the first edition of this monograph (Leonardi *et al.* 1992), the '*Birds of Western Palearctic Update*' species account (Leonardi 2001), and the '*Italian Lanner falcon Action Plan'* (Andreotti and Leonardi 2007). Data from national atlases was also included (mainly from African countries, see '*References*').

Many thanks to Neil and Liz Baker (Tanzania Bird Atlas), Joost Brouwer (Niger Bird DataBase), Rob Davies (African Raptor Surveys), Peter Browne (Mauritania Bird Atlas), Clive Mann, and Mike Jennings for supplying a large quantity of data. The main internet source was *http://www.gbif.org/*. Data were checked and analysed carefully several times in order to avoid and remove any that related to: (1) double entries (a very common source of bias), (2) erroneous locations, (3) observations of non–wild or non-native birds.



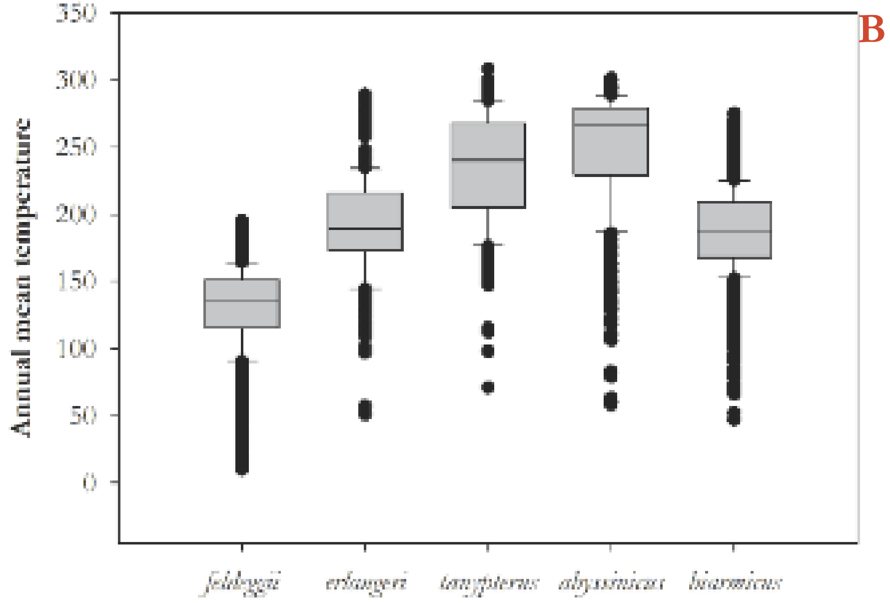


FIGURE 3.4 A, B The preferences of Lanner falcon races for altitude and annual mean temperatures. The boundaries of the box indicate the 25th and the 75th percentile and a line within the box marks the median. Dots represent outliers. *F. b. feldeggii* $n = 739$, *F. b. erlangeri* $n = 630$, *F. b. tanypterus* $n = 534$, *F. b. abyssinicus* $n = 1189$ and *F. b. biarmicus* $n = 3163$.

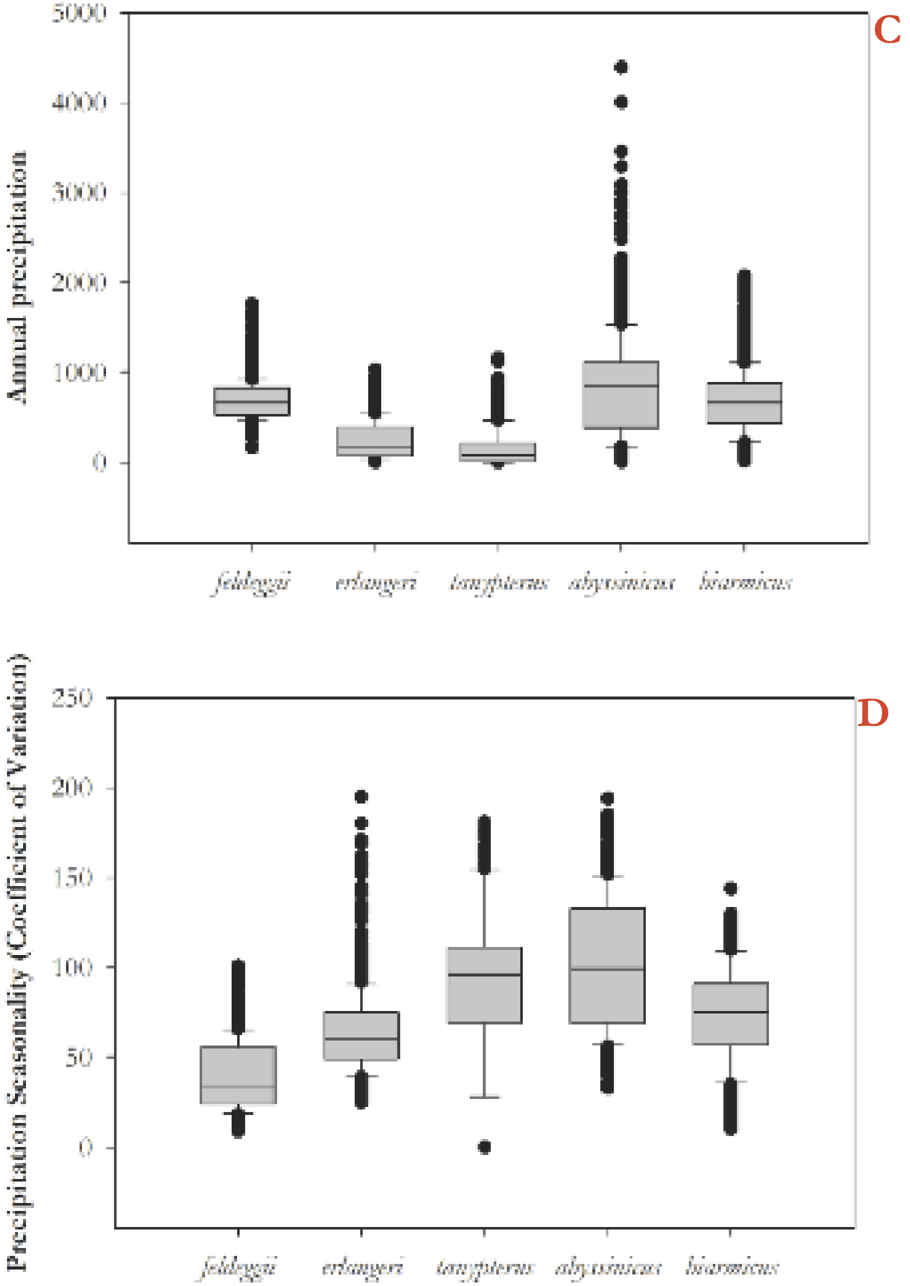


FIGURE 3.5 C, D. The preferences of Lanner falcon races for annual precipitation and precipitation seasonality. The boundaries of the box indicate the 25th and the 75th percentile and a line within the box marks the median. Dots represented outliners. *F. b. feldeggii n* = 739, *F. b. erlangeri n* = 630, *F. b. tanypterus n* = 534, *F. b. abyssinicus n* = 1189 and *F. b. biarmicus n* = 3163.

All bioclimatic data derived from the database at *www.worldclim.org*.

At the landscape level, habitat preferences are not strictly limited to requirements for breeding but also account for overall suitability for wandering birds, hence the mapped representation is of the maximum or potential distributional area (Figure s24). Each subspecies show its own clear narrow range for each of the environmental factors but with a more or less variable adaptability against their basic needs (Figure 3.4-3.5). Altitude preferences show a significant difference among races ($p < 0.05$; Dunn's Method) except for *F. b. feldeggii* and *F. b. erlangeri* ($Q = 0.893$). This similarity may be explained by the relationship between these races during the early colonization process from Southern Africa (Figure 3.2) and ultimately by genetics (see page 43). Annual temperature preferences are significant different among races ($p < 0.05$; Dunn's Method) except for *F. b. erlangeri* and *F. b. biarmicus* ($Q = 2.279$). Temperature seems to be a fundamental factor for the Lanner falcon in determining both plumage patterns (Figure 2.16) and breeding success (Leonardi *et al.* unpublished data). This strong similarity among these races is in agreement with evidence from genetics (see page 42), as well as with morphological traits (both females and males; Figure 2.26 A,B). Above all, the *F. b. erlangeri* populations in north western Africa fulfil most precisely their environmental needs as their distribution is aligned with the proposed original core area in southern Africa (Figure s25).

Rainfall shows a significant difference among races ($p < 0.05$; Dunn's Method) except for *F. b. feldeggii* and *F. b. biarmicus* ($Q = 2.214$). A high precipitation regime characterizes several territories of *F. b. abyssinicus* that could have an influence on plumage patterns as well being related to temperature (Figure 3.5 and Figure 1.16). The seasonality of precipitation was significantly different among all races ($p < 0.05$; Dunn's Method). Of particular interest is the result for *F. b. erlangeri* that highlights its preference towards very arid territories with higher temporal variability and scarcity of water resources (Figure 3.5 D). This finding may also be related to the possible seasonal movements of birds of this race into inner deserts for breeding (Jany 1960).

3.5 Potential distribution by subspecies

Overall, the predictive distributional map by subspecies accords with findings from previous literature for the Palearctic (Leonardi 2001), Africa (Brown *et al.* 1982), and the Middle East (Porter and Aspinal 2010). The main difference from previous attempts at mapping Lanner falcon populations is with regard to the identification of important core areas with very favourable environmental conditions, as well as identifying less suitable areas outside the core distribution. In addition, the predictive map shows potential areas where the species currently does not breed (Figure s25). Thus, it is based on the wider environmental needs of the species, and not solely on

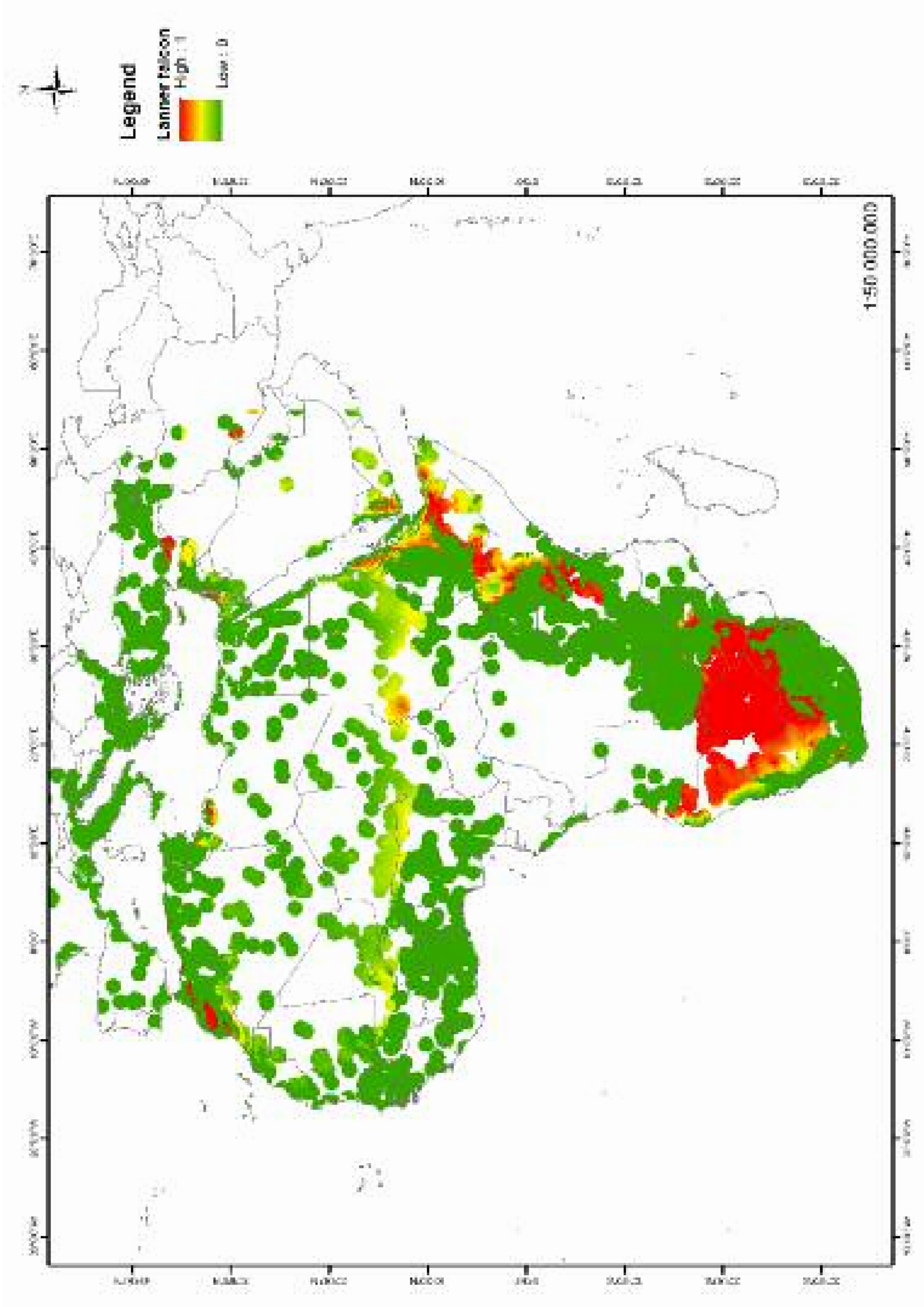


FIGURE s24 Potential distributional patterns of the Lanner falcon considered as a unique species. (n = 6255) (GIS technichal support by Mirko Amato).

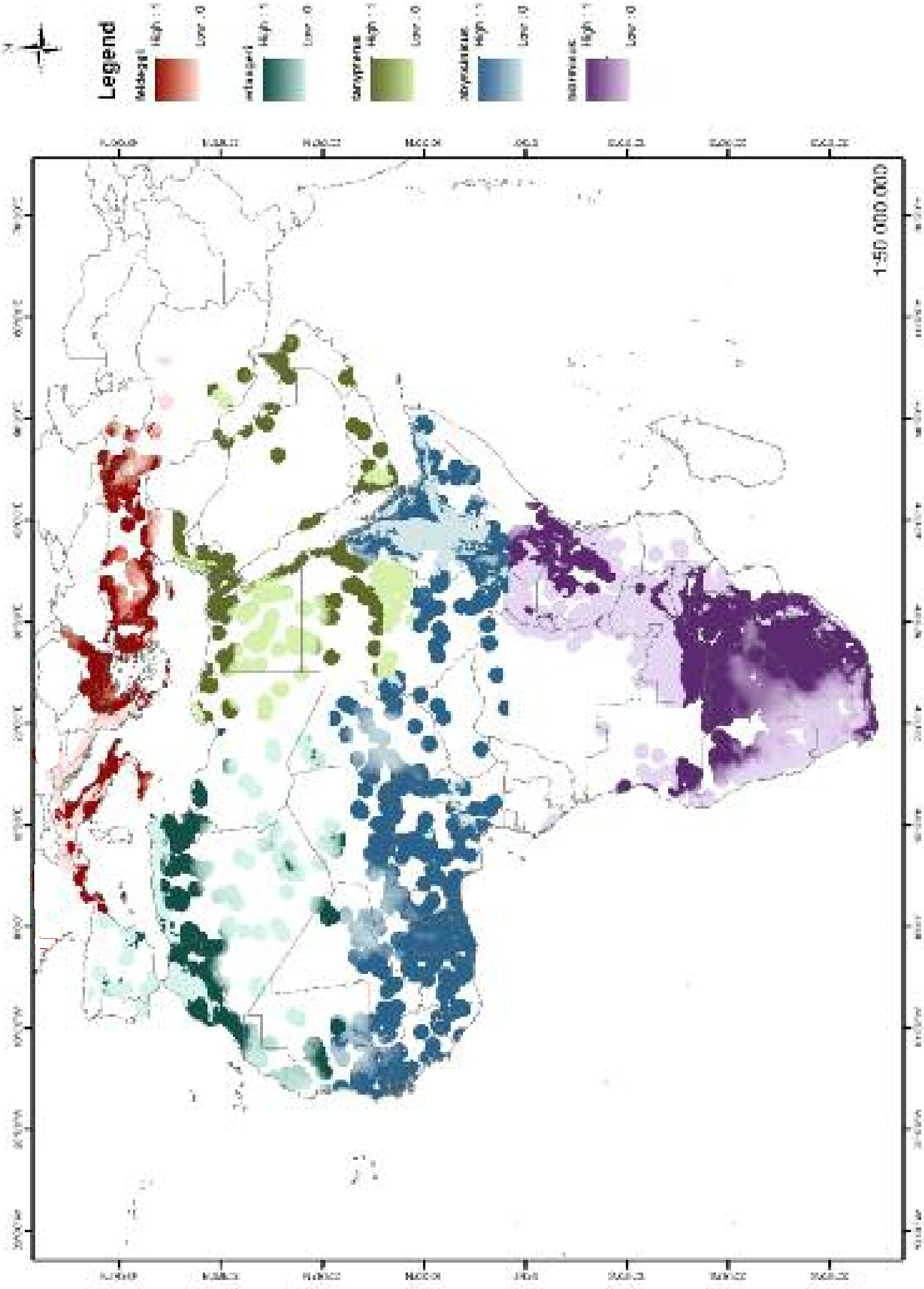


FIGURE s25 Potential distributional patterns of the Lanner falcon races (GIS technichal support by Mirko Amato).

requirements for breeding. In fact, one of the main aims of this preliminary study was to locate possible corridors for wandering birds (especially *juveniles*) which might open up new areas for colonisation, and at the same time safeguard connectivity between stable population demes.

These maps could also prove to be helpful in understanding the spatial distribution patterns of the Lanner falcon in countries where the status of the species is uncertain as well as suggesting potential contact zones between races.

Falco biarmicus feldeggii

One of the distinctive features of the *F. b. feldeggii* subspecies in the Western Palearctic is the well-known unequal size of breeding population demes (Leonardi 2001). Although it is possible to hypothesize about the dispersion process of the species (*cf.* 3.2), it is also necessary to identify which mechanisms permit the maintenance of this meta-population. As observed by Andreotti *et al.* (2008), it is not only ephemeral demes which exhibit continuous extinction–colonization cycles, but also more or less stable populations with regard to the distances between stable clusters. Thus, distances and habitat suitability at a landscape level play a fundamental role in the persistence of a sufficient number of breeding pairs to maintain a stable population (Andreotti *et al.* 2008).

Figure s25 shows two main core areas for the *F. b. feldeggii* subspecies in Mediterranean Europe: one in Italy and the other between the southern Balkans, Turkey and Caucasus. Coastal zones in the Balkans are less favourable but could be used as corridors, as could regions of northern Italy for connections to the east (Veneto) and west (Piemonte). The map also reveals that southern France and the eastern portion of Hungary also contain habitats suitable for the Lanner falcon. In most cases, the regions revealed by the model are reached more or less frequently by wandering individuals.

The main core area in the southern Balkans includes Macedonia, central and northern Greece, and Bulgaria (Figure s25). A potential eastern area is the border with the Black Sea, Bulgaria and Romania. The western connection seems to be not so feasible as has been supposed in the past for individuals from the Balkans that arrive more or less regularly in Italy (Valentini 1957).

Greek and Turkish populations are geographically very close but it is not easy to assess if a source-sink system exists. Unfortunately for the time being, there are no plausible estimates for the number of breeding pairs in Turkey (Leonardi 2001) but the model, as expected, shows large zones in the country that would be suitable habitat for the Lanner falcon. A source role for a Turkish population could feasibly explain the ephemeral breeding populations in Caucasus and also in northern Iran (Scott 2008, Abuladze 2013).

Falco biarmicus erlangeri

As expected, the model confirms the core area for this race that includes Morocco, North Algeria, Tunisia, and Tripolitania (Figure s24). A very sparse less suitable area covers the Sahara desert from the Western Sahara, through Mauritania, Mali, South Algeria, and into Libya. Tamanrasset and the Tassili National Park in southern Algeria are small core areas surrounded by plain desert land (Figure s25). Contact zones with *F. b. abyssinicus* include Mauritania, Mali, Niger, and Chad. In particular, the Tagant region (Tichit, Mauritania), Adrar de Ifoghas (Kidal region, Mali), Aïr Mountains (Agadez Region, Niger), and Tibesti mountains (north Chad) are key areas where these two subspecies overlap. Records of the passage of wandering *F. b. erlangeri juveniles* through Gibraltar from Morocco as well as of some breeding attempts in the past (*cf.* 1.2) confirm that the Iberian peninsula is suitable for colonization. Although Andalucía and south Portugal are the main regions reached by these individuals, the model also identifies Alicante province as being close to providing the main habitat preferences of this race (Figure s25).

Falco biarmicus tanypterus

As with *F. b. erlangeri*, the distributional model map for *F. b. tanypterus* is very close that created by previous attempts at mapping the species distribution (Porter and Aspinall 2010). The most favourable zones are the northern belt including Cyrenaica (Libya), the Qattara depression, the Cairo region, and the Sinai peninsula (Egypt), southern Israel, and the Aqaba and Ma'am governorates (Jordan; Figure s25). In addition, a large area including the desert zones of Syria (Homs region) bordering Iraq is shown to provide ideal habitat. The eastern Sahara desert between Egypt and Sudan is sparsely occupied with some more favourable locations found in North Sudan. A southern belt include western Darfur, Kordofan, the Khartoum region, and Port Said in the Red Sea (Figure s25). Contact zones with *F. b. abyssinicus* include western and southern Darfur, a large area bordering South Sudan, the Sennar region, and the Eritrean border. The Arabian peninsula shows scattered distributional areas with a stronghold in Yemen as part of a large suitable zone with the countries of the Horn of Africa (Figure s25). Of particular interest are the potential areas of suitable habitat in the Bushehr and Fars regions of Iran (Figure s25).

Falco biarmicus abyssinicus

The core areas in Eastern Africa for the *F. b. abyssinicus* subspecies are North Uganda, North Kenya, Ethiopia, Eritrea, and northern Somalia (Awdal, Woqooyi Galbeed, Togdheer, Sanaag and Bari regions) (Figure s25). The Rift Valley and surrounding zones represent the most important corridor and suitable territory for the race but also for the species as a whole (Figures s24 and s25). Towards the west, the region to the south of Darfur seems to be an important contact region along with northern Cameroon and Nigeria. The distribution in West Africa is strongly fragmented and perhaps suffered from a fewer number of sightings. In fact, the core areas are not at all clearly identified. It is also evident that the influx of the semi-arid climate of the Sahel in countries between the Sahara Desert the Sudanian Savanna has had an influence on the observed distribution patterns (Figure s25).

Falco. biarmicus. biarmicus

The map rendering for the nominate race is well defined due to the large number of available records and sightings of this subspecies. Eastern South Africa, Lesotho, Botswana, Zimbabwe, and Southern Zambia form the key parts of a very large core area (Figure s24). When considering the Lanner falcon as a unique species, the core area tends to be restricted to Botswana and its surroundings including a large part of Namibia (Figure s25). Populations in southern Kenya and Tanzania play a fundamental role in connecting to southern Africa via the Rift valley (Figure s24 and s25).

Figure s26 Dorsal view of a perched adult *F. b. abyssinicus* (Ethiopia). © and courtesy of Péter Csonka.

Chapter 4.
Territory and breeding densities

4.1 Main habitat types

For the most part, the Lanner falcon occupies mainly open areas ranging from xeric to mesic environments, from shrubs and steppe to plain desert zones, but also montane grasslands (Tarboton and Allan 1984, Chiavetta 1992). In Africa, it also chooses predominantly open habitats ranging from forest edges to desert, and it is most commonly found in open savannah and grassland although it can also be found in the depths of the Sahara and Namib deserts (Brown *et al.* 1982). In Tunisia as well as in Sicily, the species can usually be found on cliffs and rocky ground, although it is more often observed on open plains at some distance from any mountainous terrain (Whitaker 1905, H. Azafzaf pers. comm.). Nevertheless, in very open areas it would suffer from the lack of suitable cliffs for nest sites (Brown *et al.* 1982). In South Africa, agricultural activities have very positive effects on the abundance of the species due to the creation of more open areas and farmland in place of woodland, thereby increasing the number of breeding sites (such as old crow nests) as

Figure 4.1 The breeding habitats of the Lanner falcon (*F. b. feldeggii*) with large open lands in Macedonia © and courtesy of Bratislav Grubač.

well as the abundance of preferred prey (Tarboton and Allan 1984). The Lanner falcon is absent from the equatorial rainforest. Nevertheless, it has also been observed at an altitude of 2450 metres in the impenetrable Bwindi Forest of the Ruhinda Ridge in Uganda. It seems that Lanner falcon pairs can use cliffs or rocky pinnacles surrounded by native forest such as on Mount Elgon in Kenya, the Manho Forest surrounding Mount Namuli in Mozambique, as well as in densely inhabited but formerly forested country in Kenya and Ethiopia (Brown *et al.* 1982, Lewis and Pomeroy 1989, Dowsett-Lemaire 2008). The same can be said of Soutpansberg in northern South Africa, where the Lanner falcon breeds on cliffs overlooking thick forest (Jenkins 1994), as well as in Zambia, where sightings of birds are usually over woodland and occasionally hunting over open grasslands (Benson *et al.* 1971). Overall in Eastern Africa, the Lanner falcon seems to show a preference for dry open country, scrubland, and sparsely wooded grasslands (Britton 1980).

Falco biarmicus feldeggii

In Italy, preferred habitats include pasturelands, steppes, and uncultivated fields with small cliffs near open valleys (Chiavetta 1992). In Sicily, extensive wheat fields in the south are replaced further northwards by citrus groves and olive yards (Ciaccio *et al.* 1989, Leonardi 1994). Natural vegetation consists of interspersed herbaceous steppe-like fields inside monoculture, and Mediterranean shrubs in olive yards (Ciaccio *et al.* 1989; Figure s28). A precise description given by Salvo (1984) of a preferred habitat in central southern Sicily includes dry badlands or open uncultivated valleys covered by herbaceous vegetation used for grazing and partially cultivated with cereals, olive and almond trees, and vineyards. In Macedonia, breeding pairs inhabit mainly oak scrublands (47%) and dry pastures (33%), less degraded oak forest (0.7%), arable land (0.7%) and Mediterranean pseudo-maquis (0.7%; $n = 15$; Figure s27; Grubač and Velevski 2010). Mebs (1959) was among the first to note the importance of open habitat surrounding nesting sites for *F. b. feldeggii* in Sicily. In Crete a nest was placed in a rocky gorge with sparse bushes and small trees, while in Rhodes the nesting site was on a low mountain covered with *Pinus* woodland similar to a nest in the Dadia forest in Thrace (Handrinos and Akriotis 1997). In the Gargano Peninsula (Apulia, southern Italy), the preferred habitat was mainly steppe-like fields but also river valleys covered by patches of xeric vegetation (2 pairs out of 7; Talamo 1998, Caldarella *et al.* 2005). Records in Turkey are from arid steppe regions and treeless, montane zones, (Kirwan *et al.* 2008). In Southern Tuscany, the species has been recorded in rocky habitats with xeric and mesic grasslands, as well as xerothermophilous and mixed forests (Giovacchini 2003).

The habitat preferences of *F. b. feldeggii* in the Caucasus are of particular interest as they consist of open or semi-open arid semi-deserts in eastern Georgia, and wor-

Figure s27 Preferred *F. b. feldeggii* habitat in Macedonia. © and courtesy of Bratislav Grubač.

Figure s28 Preferred *F. b. feldeggii* habitat in eastern Sicily. © and courtesy of Stig Frode Olsen.

mwood-absinthe semi-desert and mountain steppes in Azerbaijan (Abuladze 2013). These semi-deserts are fragmented by arid woodlands, savannah-type vegetation, and low but steep rocks, ravines and hills (Abuladze 2013).

Falco biarmicus erlangeri

In north-west Africa, the Lanner falcon can be found inhabiting the '*southern slopes to the Atlas, and the semi-desert country stretching away to the south of those mountains, where stony plains, bounded by arid cliffs, succeed each other in terraces, gradually dropping down to the level of the Sahara*' (Whitaker 1905). In the Moroccan Zaer and Plateau areas, rocky cliffs dominate Mediterranean scrublands (Bergier 1987). Considered to be rare in woodlands, the species is more often to be found inhabiting open lowland steppes and pistachio orchards particularly in eastern Morocco, as well as more barren areas such as Haouz and the *Acacia raddiana* plains of the Western Sahara (Bergier 1987). The species can also be found nesting in the Serir Tibesti region of southern Algeria, where nest sites were surrounded by bare soil without any vegetation and at were located at least fifty kilometres from the nearest oasis (Figure s29; Jany 1960).

Falco biarmicus tanypterus

In northern Yemen this species is usually observed around steep cliffs, but can also be seen hunting over the montane plains and the Sebkha (Philips 1982). Lanner falcon pairs are also capable of breeding in hyper-arid areas of the eastern Sahara, such as Darb el Arba' and the Lybian desert, that receive less than five millimetres of rainfall per year (Figure s30; Goodman and Haynes 1992). In Israel, the species is typically resident in the desert, ranging from Eilat in the south to the Samarian Desert in the north (Yosef 1988). In Sudan and South Sudan, the species exhibits a preference for dry open bush savannah (Nikolaus 1987) although a pair have been observed habitually frequenting the palm-groves of Khartoum (Butler 1905).

Falco biarmicus abyssinicus

In Cameroon, the Lanner falcon occupies predominantly savannah districts, and has been recorded mainly during the dry season, although it has also been found in forested areas (Holyoak and Seddon 1990). In the Bamenda Highlands of Cameroon, habitat preferences range from intensively grazed pastures dominated by *Sporobolus africanus* and *Pennisetum cladestinum* with sparse shrubs and ferns, lightly-grazed pastures, tall grasslands dominated by *Hyparrhenia* sp., as well as rocky grasslands and slopes (Sedláček *et al.* 2007). In Ghana, the species has been observed in the forest zone, in farm bush and near large rivers in the northern and coastal areas, but has

FIGURE S29 Preferred *F. b. erlangeri* habitat in southern Algeria. © and courtesy of Redouane Tahri.

FIGURE S30 Preferred *F. b. tanypterus* habitat in a desert area of Libya. © and courtesy of Yuonis Al Madani Said.

not been noted in the western half of the forest zone (Dowsett-Lemaire and Dowsett 2014). In Burkina Faso, the species can be found in habitats ranging from town gardens and wooded regions, to rocky areas, watercourses and fields (Pavia *et al.* 2012). In Liberia, the species seems to be expanding its range southwards as a result of deforestation resulting in the conversion of forests to man-made savannas (Gatter 1997). In Nigeria, the species has been observed on steep rocky hills, over open savannah, and also in more urban areas (Hartert 1912, Elgood 1982). In Senegal, the Lanner falcon can be found on rocky cliffs surrounded by savannah with patches of grass and shrubs, and semi-deciduous forest in the foothills (Figure s31). In the Central African Republic, habitat preferences are for *Terminalia laxifolia* savannah woodland, forest, and mixed lowland savannah woodland (Carroll 1988). In Ouadi Rimé-Ouadi Achim Faunal Reserve in Chad the preference seems to be for wooded areas and it is virtually absent from the open steppe (Newby 1979).

Falco biarmicus biarmicus

In Southern Africa, the Lanner falcon shows a preference for a wide range of open habitats ranging from Afro-alpine grasslands (in the Sehlabathebe National Park of Lesotho for example) to the Kalahari desert (Figure s32; Jenkins 1995, Kopij 2002). Observed at altitudes of up to 2100 metres on Mount Kilimanjaro, the species occupies forest edges and cultivated areas adjacent to forests and conifer plantations (Cordeiro 1994). In South Africa it is frequently found in open areas where there are suitable cliffs for breeding and not too much bush about (Finch-Davies 1920). In Botswana, the species has been recorded in tree and bush savannah in lush and semi-desert conditions, as well as along the edges of woodland, pans, and plains (Penry 1994). In Uganda, habitat preferences seem to be for open country, especially with some cliffs, and the species can be found even up to the edge of the forests as well as in the drier areas in the western district of Kenya (Mann 1976, Carswell *et al.* 2005).

In Angola, habitat preferences are for *Acacia* sp. and *Brachystegia* sp. woodlands, rocky hills and open semi-arid shrub-lands with scattered trees (Dean 2000). One of the most important crop-types inside territories is wheat, which attracts large numbers of Red billed Quelea during late winter and early summer. This in turn attracts various raptors, including the Lanner Falcon (Anderson 2000). In Zimbabwe, the species has been recorded in denuded woodland, tree savannah, heavily grazed lands and ploughed farmlands (Irwin 1981, Thomson 1984). In the Nyika National Park in northern Malawi, the species can be found over the high plateau and is often attracted to grass fires for feeding (Dowsett-Lemaire 2006). The Lanner falcon has also been observed in mangroves, coastal scrub, and at salt pans in the Dar es Salaam area of Tanzania (Harvey and Howell 1987). In central Mozambique, rocky outcrops

Figure s31 Preferred *F. b. abyssinicus* habitat in south-eastern Senegal. © and courtesy of José María Fernández-García (Jane Goodall Institute).

Figure s32 Preferred *F. b. biarmicus* habitat in Tankwa Karoo, South Africa. © and courtesy of Jannes Kruger.

and woodland on the plains are favoured (Parker 1999). Other recorded habitats include the forest fragments of the Taita Hills of south eastern Kenya, and the crater highlands and open arable and grasslands of Ol Molog in Tanzania.

Quantitative studies

To date, only two scientific papers have been entirely devoted to a quantitative analysis of the distribution of the Lanner falcon at a landscape level. One study was carried out in South Africa (Jenkins 1994) and the other in Italy (Andreotti *et al.* 2008). The former also made a comparison among breeding and non-breeding seasons, while the latter also contributed a spatial analysis of population connectivity (Jenkins 1994, Andreotti *et al.* 2008).

In South Africa, the Lanner falcon occurred in 51% of squares surveyed whereas in Italy the figure was only 6.4% (Jenkins 1994, Andreotti *et al.* 2008). In South Africa, the species exhibited a preference for high cliff areas (at least one cliff higher than one hundred metres) during the breeding season (Jenkins 1994) while during the non-breeding season, the nominate race enlarged its range by movements into flat, open areas without cliffs especially in the Karoo and the southern Kalahari (Jenkins 1994). Similar short, local movements towards flat areas and wetlands were also reported in Italy, although to a lesser extent (Andreotti and Leonardi 2007). The main breeding habitats reported in South Africa include mesic woodlands, grasslands (especially sour grasslands), and the Fynbos shrubland of the Western Cape (Jenkins 1994). Nevertheless, the species would seem to be a habitat generalist as the selection of vegetation types is contingent on the relative availability of cliffs (Jenkins 1994).

In Italy, it mostly occupies territories between 200-500 m above sea level (44%), an annual rainfall between 600-800 mm (62%), human presence of between 50-150 inhabitants per square kilometre (63%), and extensive cultivated areas (73%; De Lisio *et al.* 2006, Andreotti *et al.* 2008). Altitude would seem to be the most important factor at all levels of spatial clustering of breeding populations, in association with climate, precipitation, and vegetation (Andreotti *et al.* 2008). The density of human habitation and habitat composition seem to have little effect at the landscape level (Andreotti *et al.* 2008) although in the Georgian Caucasus the same subspecies (*F. b. feldeggii*) seems to actively avoid nesting in areas prone to human disturbance (Abuladze 2013).

4.2 Habitat preferences

This section includes published data relating preferred habitats at a more local level, as opposed to the landscape level. For a comprehensive overview of habitat preferences as the landscape level see section 3.3 and the associated figures (Figures 3.4, 3.5). Several environmental parameters relating to breeding sites have been described in the literature including altitude, aspect, and orientation (Figure 4.2; Leonardi *et al.* 1992, Leonardi 2001).

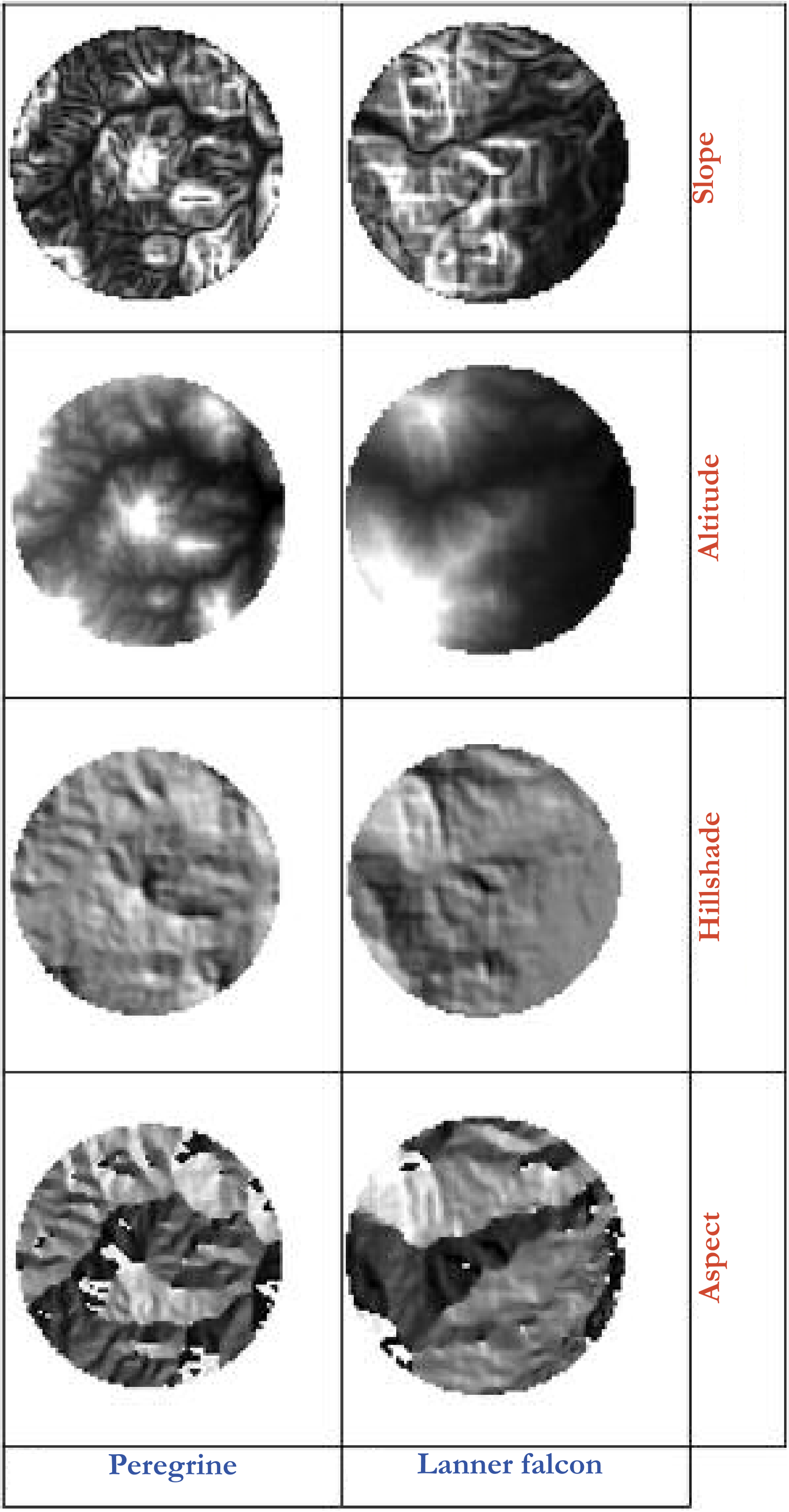
Altitude

As mentioned above, breeding pairs in Italy mostly nest below 1000 m, between 60–400 m in Calabria for instance, although a nest was found at 1125 m which was surrounded by three Peregrine nesting sites (Mirabelli 1982, Chiavetta 1992). In the Emilia-Romagna region (towards the northern limit of the species distribution) nest sites are located at altitudes of between 300 and 600 m (Chiavetta 1982). Many data in the literature make reference to sightings outside the usual altitudinal range of nesting sites. Breeding pairs have been recorded at 1500 m in Asni, and some sightings have been made at 2600 m in the Oukaïmeden region of Morocco (Barreau and Bergier 2001). Three breeding pairs were found at an altitude of 3200 m on Mount Elgon in Kenya, in giant heather along a stream in the lower moorland or heath zone (Britton and Sugg 1973, Carswell *et al.* 2005). At Lake Deemtu in Ethiopia an individual was recorded at 3890 m (Ash 1977) and one individual at Mehal–Wenz was recorded at 2250 m. In Tizi'n Zaker, in Morocco, records extend to 2500 m and up to 4250 m in Ethiopia.

The nominate race was recorded occupying sites ranging from highveld grasslands at 2100 m at Dullstroom, to lowveld at 700 m at Mangake, in the Kruger National Park (Tarboton and Allan 1984). A pair has been recorded at 2000 m in the Ngamat area of the Crater Highlands, Tanzania, as well as a pair at Londorossi Park Gate at 2100 m on Mount Kilimanjaro in Tanzania, and at 1650 m at Mbulumbulu in the nearby Arusha region. In contrast the species has not been recorded in the eastern highlands of Zimbabwe above 1500 m and in Saudi Arabia, *F. b. tanypterus* prefers territories at altitudes of between 700–1000 m.

For *F. b. feldeggii* high altitudes have been considered as a strong limiting factor for reproduction based on studies at the Sibillini National Park in central Italy (Manzi and Perna 1994). A recent study conducted in Sicily revealed a strong correlation between altitude and nest-site quality, expressed in terms of both occupancy and productivity (Amato *et al.* 2014). This study found that low quality sites were typically found at high average altitudes of around 554 m, whereas high quality sites tended to be located at lower altitudes of around 391 m (Amato *et al.* 2014). Nevertheless, one of the most important factors influencing breeding performances of *F. b. feldeggii*

FIGURE 4.2 An example of the differences between the characteristics of territories (hill aspect, shade, altitude, and slope) between Lanner and Peregrine falcons in eastern Sicily in Italy. (GIS technical support by Mirko Amato).


Slope
Altitude
Hillshade
Aspect
Peregrine
Lanner falcon

is the slope of the nesting cliff (Amato *et al.* 2014).

Slopes

The mean slope of the nest territory is an important predictor for differentiating the selection of cliff sites by the Lanner Falcon, together with the slope of the nest-site and the mean elevation of the area (Figure 4.3; Amato *et al.* 2014). In addition, there is a significant direct effect of the slope of the nest-site on the mean fledgling number per successful breeding pair (Amato *et al.* 2014). Finally, slope values also help to distinguish between the selection of cliff sites by Lanner and Peregrine falcons (Figure 4.3; Amato *et al.* 2014).

As observed for the nominate race, it would appear that even on small vertical faces situated on large slopes, Lanner falcons can approach and depart to and from the nest site with a minimum of energy expenditure by gliding and using updraughts (Stephenson 2001). Large cliffs always had some air movement, which the birds could use to gain lift, whereas on small cliffs Lanner falcons had to employ flapping initially, at least until they made it to a ridge where they could exploit the air currents (Stephenson 2001). It is possible that the slope of the ground around the eyrie and the mean incline of the surrounding area have an influence on energy expenditure during the breeding season that could ultimately improve provisioning rates at nests (Jenkins 1992, Amato *et al.* 2014).

Rainfall

One of the main assumptions with regard to the Lanner falcon, based on its presumed African origins, is the preference of the species for territories with low precipitation regimes (Leonardi *et al.* 1992). However, results from landscape habitat analysis reveal that this tendency is only shown by the *F. b. tanypterus* and *F. b. erlangeri* races where a proportion of the breeding pairs regularly use arid to hyper-arid environments (Figures s29 and s30) such as the rocky, Saharan-massif terrain of the Ennedi, Tibesti and Air Mountains in Chad and Niger, where rainfall is limited to just a few millimetres per year (Newby 1981). Lewis and Pomeroy (1989) observed the virtual absence of the Lanner falcon from even slightly moister areas of the coastal lowlands of Kenya, and also from the higher rainfall areas in the highlands. Therefore, populations seem to be geographically limited (39°E) by precipitation regimes of above 500 mm and, in fact, apart from Turkana, the Lanner falcon only occupies arid environments adjacent to semiarid regions (range 250–1000 mm; Lewis and Pomeroy 1989). This factor may explain the scarcity of the species in higher-rainfall areas such as the Northern and Luapula Province of Zambia (Dowsett *et al.* 2008). Nevertheless, as can be seen in Figure 3.5 D, seasonal variation in precipitation re-

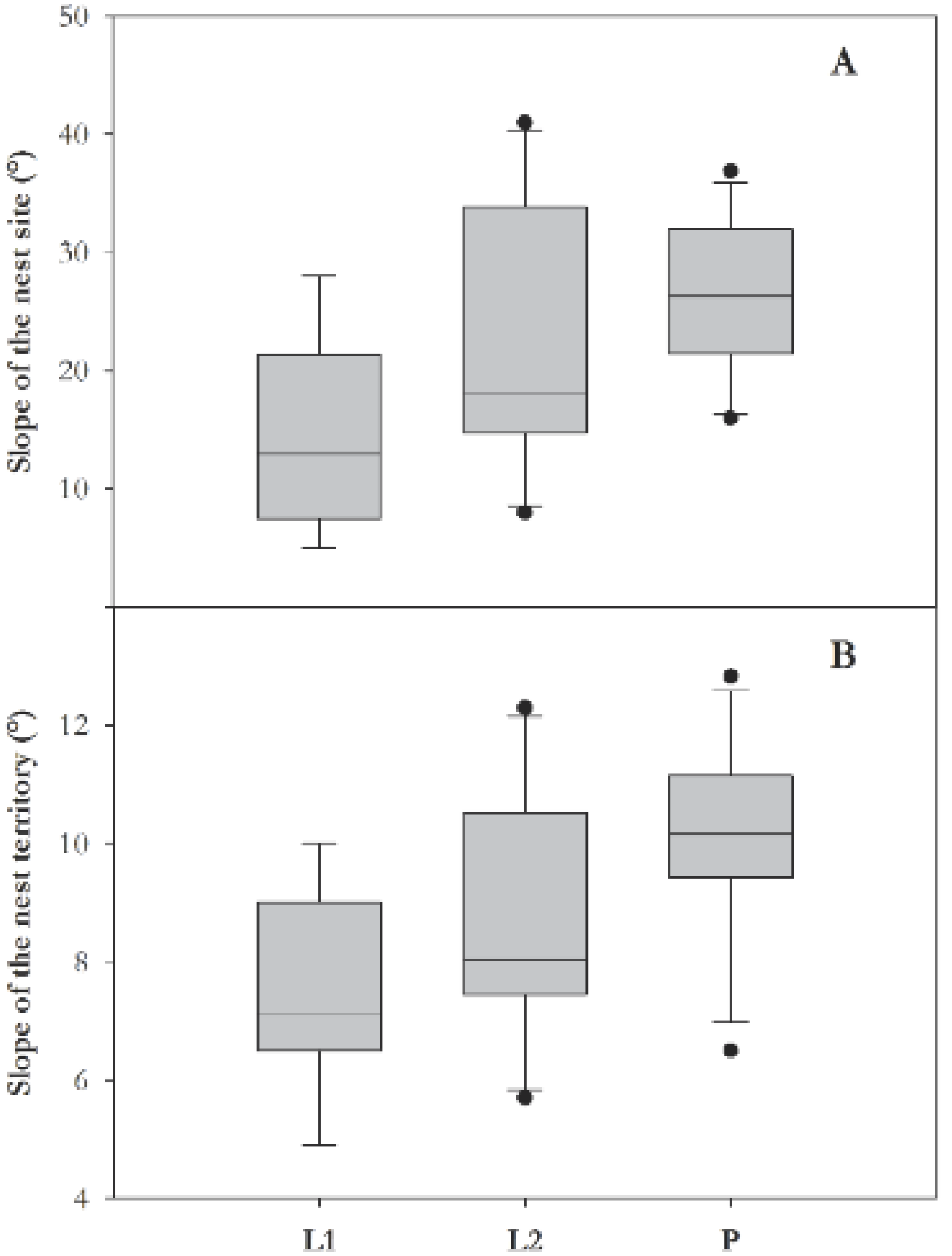


FIGURE 4.3 Comparisons between the slope of the nest sites (A) and the slope of the nest territory (B) for both Lanner falcons and Peregrine falcons in eastern Sicily in Italy. P = Peregrine falcon nest-site. Lanner falcon nest sites were separated into high (L1) and low (L2) occupancy.

gimes may gimes may influence the breeding biology of the Lanner falcon in areas such as in Masite and on the Qeme Plateau of Lesotho which exhibit different densities of nesting pairs in dry and wet seasons (Kopij 2010).

4.3. Habitat features of nesting sites

Several studies have measured habitat characteristics surrounding Lanner falcon nesting sites (Figure 4.4 A-D). Unfortunately, these findings mainly relate to *F. b. feldeggii* and *F. b. biarmicus* and such analyses for the other races await further study.

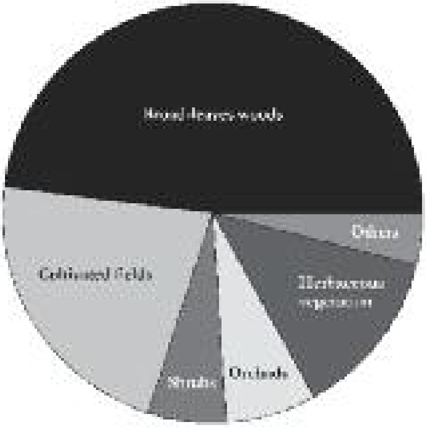
In areas of central Italy such as in Molise and Latium, breeding pairs tends to preferentially occupy sites with lower percentages of all kind of wooded areas, and with increasingly open cultivated or uncultivated fields (De Lisio *et al.* 2006). Thus, areas with herbaceous vegetation cover could account for up to 40% of nest sites as in Latium, or more than 60% in Sicily, and appear to have a great influence on nest site selection (Dipasquale 2005, Brunelli and Sarrocco 2013). At a landscape level, this tendency is also evident along the latitudinal gradient from northern regions to Sicily, and hence from low to high densities of pairs (Figure 4.4 C). Other positive correlations also exist between nest site selection and sites at low altitudes in areas of warm temperatures as mentioned above, (see section 4.2; De Lisio *et al.* 2006).

The Lanner falcon (*F. b. biarmicus*) in Zimbabwe is an open country species whose range has probably increased as a result of recent deforestation in Africa (Hartley 2000). In this country, 231 nesting pairs were detected as part of a study on habitat characteristics of breeding sites (Hartley 2000). Overall, 56.4% of pairs occupy ranchlands where the natural habitat was relatively undamaged and densities of human population was low, 32.9% in poor quality habitats associated with deforestation and increasing human presence, and only 10.6% in protected areas covered by forest (Hartley 2000). A total of more than 65% of Lanner falcon pairs were found in open and woodland habitats of the granite shield, including rock formations such as kopjes, tor, and domed inselberg (Figure 4.4 D; Hartley 2000).

A first quantitative study on habitat fragmentation support the importance of open lands surronding Lanner falcon nesting sites in Eastern Sicily. In fact, reduced patch size of uncultivated fields have a negative influence on main prey densities (e.g. pigeons) and that in turn have an indirect effect on parental efforts (Dipasquale 2005).

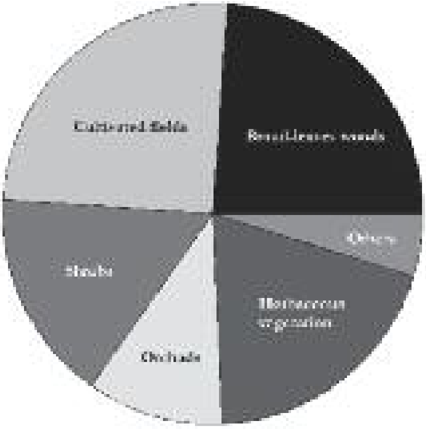
4.4 Territorial behaviours and competitors

A variety of more or less aggressive displays towards intruders, as well as instances of piracy, have been described from several parts of the Lanner falcon distribution range. Unfortunately, to date no quantitative studies have been carried out in order



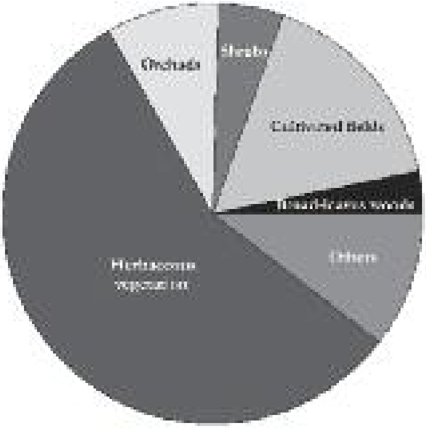
A

Latium (Central Italy)



B

Abruzzi (Central Italy)



C

Eastern Sicily
(Southern Italy)

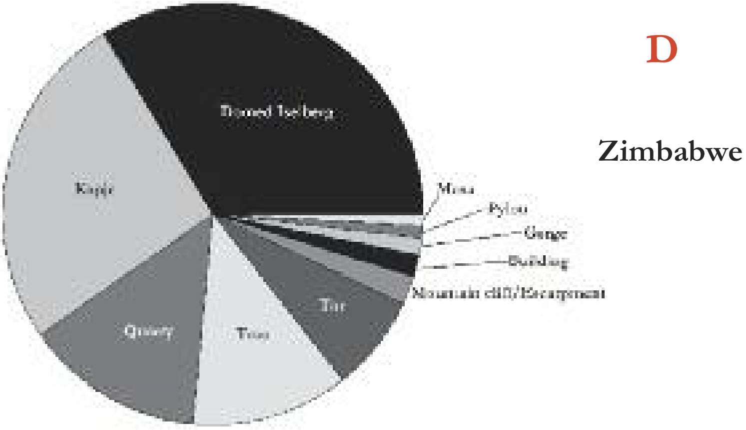


FIGURE 4.4 Differences between the habitat composition of Lanner falcon territories surrounding nest sites in central Italy (Latium and Abruzzi), southern Italy (Sicily) and Zimbabwe (Hartley 2000, Dipasquale 2005, De Lisio *et al.* 2006, De Sanctis *et al.* 2009, Brunelli and Sarrocco 2013).

to ascertain the relative effectiveness of these defensive behaviours in terms of costs and benefits.

Conspecifics

Reports with regard to aggressive displays shown by breeding pairs in establishing and maintaining a stable territory remain very few and scattered. It is probable that the inconspicuous and relatively infrequent nature of these behavioural patterns by the Lanner falcon has biased the encounter rate in the field. For example, the Lanner falcon is generally considered a quite quiet falcon in comparison to the Peregrine (Cramp and Simmons 1980, Leonardi *et al.* 1992). Nevertheless, a recent quantitative analysis has revealed a number of calls uttered, especially by males, during the courtship and nest selection (Leonardi *et al.* 2013). These calls could be considered as an '*honest signal*' for the quality of males which would presume competition between birds for the best territories (Leonardi *et al.* 2013). Thus, attack frequencies towards conspecific competitors, both adult and young, would be largely dependant on the relative densities of breeding pairs (Figure s33). In areas where a low recruitment rate persists among young or un-paired birds, these could well hold and own a sub-optimal breeding territory (Leonardi *et al.* 2013, Amato *et al.* 2014).

Aggressive displays consist of fast attack stoops and leg-lowering, harsh calls, and gliding briefly alongside the adversary in a threat posture with wings held at a high dihedral (Kemp 1993). The frequency and nature of attacks is dependant on stage of the nesting phase, and aggression towards young birds increased in April, and between pairs of adults in May in South Africa (Figure 33; Kemp 1993). Nevertheless, a young bird roosted very close to an established nest (within 800 m) during courtship and even after breeding had started (Kemp 1993). Interestingly, in captivity, a female adult tends to have a strong aggressive tendency towards its immature mate (Snelling 1973).

In central southern Sicily, mean nearest-neighbour distance (NND) is around five kilometres but hunting territories are presumably separate as the average distance moved from the nest when foraging is only two kilometres (Salvo 1984). In the Kalahari, an apparent territorial dispute observed between two pairs produced some spectacular aerobatics (Winterbottom 1969). In the forests of Mozambique, pairs were observed to be very aggressive towards other Lanner falcons and raptors (Dowsett-Lemaire 2008). In winter 1902 in the palm-trees around Khartoum an unusually high density of birds in this favourable habitat permitted an increased level of recruitment into the population (Butler 1905).

Small falcons

In terms of interactions with small falcons (mainly kestrels and hobbies), it is difficult to differentiate between territorial displays and effective predation (see Chapter 7). Many nest-sites are shared with kestrels, an example of which can be found in Tunisia where the ruins of the Roman aqueduct near Tunis are used by Lanner falcons as well as by colonies of Lesser Kestrel (Azafzaf 1999). In a nest in Tuscany, a nest of Common Kestrel and a colony of Jackdaws can be found five hundred metres from a Lanner falcon nest (Morimando *et al.* 1997). In Sicily, Lesser Kestrels were present at several cliff-sites with no reported instances of inter-species aggression, whereas according to Salvo (1984) the Common Kestrel shared at least a fifth of the cliffs with Lanner falcons whose main nest distance less than 300 m away, and sometimes attacked the Lanners (Salvo 1984, Ciaccio *et al.* 1989).

Kemp (1993) reported several interesting details concerning relationships between Lanner falcons and the Greater Kestrel (*F. rupicoloides*) near Pretoria in South Africa. Lanner falcons appeared as the dominant species and chased (and possibly preyed upon) the Kestrels, effectively controlling their territory and affecting their spatial patterns and breeding phenology (Kemp 1993). In this case, following a year when the Lanner falcons were absent, two new pairs of Kestrels established nests at the site (Kemp 1993). Of all of the observed aggressive interactions at this site, 28% of the attacks were initiated by the Greater Kestrel, 28% elicited no response, and 44% of the attacks came from the Lanner falcons aimed towards the Greater Kestrels (Kemp 1993). The female Kestrel only attacked Lanner falcons perched on

Figure s33 Fighting among sub-adult and adult *F. b. biarmicus* in Kgalagadi Transfrontier Park, South Africa. © and courtesy of Johann Grobbelaar.

Figure s34 A *juvenile F. b. biarmicus* harassing a Black-backed Jackal *Canis mesomelas* at a water hole in the Kgalagadi Transfrontier Park © and courtesy of Brett E. Ellis.

pylons and mainly during the period when nestlings were present at the nest, and at a similar site where Lanner falcons nest in a pylon-sited nest they are avoided altogether by Greater Kestrels (Hustler 1983). Interestingly, Greater Kestrel chicks were heard to give a whining chirr call at a passing Lanner falcon when it came close to their nest (Hustler 1983).

A position of dominance is also reported in the case of the Taita falcon *F. fasciinucha* in Uganda where three breeding pairs of Lanner falcon occupied three sites formerly occupied by the smaller falcon (Carswell *et al.* 2005). In Zimbabwe, Taita falcons seem to restricted in the areas they occupy and, along with Peregrine falcons, shared well-wooded zones along river systems that are avoided by the Lanner falcon (Hartley 2000). The same Author was of the opinion that the Lanner falcon appeared to have benefitted from land clearance within forests, unlike the Peregrine and Taita falcons present in the same areas (Hartley 2000). In Ghana, cliffs were frequently occupied by other species of falcon such as the Fox Kestrel (*F. alopex*) and Lanner falcons were only observed in adjacent cities and lowlands (Dowsett-Lemaire and Dowsett 2014). In a small inhabited rocky island in the south Aegean Sea where around 200 pairs of Eleonora's falcon bred, between 8–70 individuals of this social falcon were observed at least eight times mobbing any Lanner falcons that approached the nesting area (Wink and Ristow 2000).

Large raptors

Interactions between Lanner falcons and other large raptors include competition for nest-sites, aggressive behaviour, piracy, and predation, both as predator and as prey. In South Africa during the nesting season, both parents or sometimes both mates were observed attacking individuals of a number of other species including Black Crows *Corvus capensis*, Black Kite *Milvus migrans*, African Marsh Harriers *Circus ranivorus* and also other large raptors such as Wahlberg's Eagle *Aquila wahlbergi* and Black Eagle *A. verreauxii* (Kemp 1993). On the other hand, Blackshouldered Kite *Elanus caeruleus* and Bearded Vulture *Gypaetus barbatus* were observed attacking Lanner falcons in response to acts of piracy (Kemp 1993). A female Ovambo sparrowhawk *Accipiter ovampensis* was seen to crouch flat on the nest in a defensive position when Lanner falcons passed low overhead (Kemp 1975a). On the Jos Plateau in Nigeria a pair of *F. b. abyssinicus* were recorded harrying a Red-tailed Buzzard *Buteo auguralis* at a distance of 300 m from their nest, and were also observed attacking a Pied Crow *C. albus* and when one of the Lanner falcons struck the crow on the head, the crow died from the subsequent fall from the air (Ebbutt 1964).

Numerous observations have been made of aggressive interactions with the Black Eagle during the breeding season in supposed competition for nesting sites (Gargett 1971). In Botswana, for example, on the same cliff Black Eagles, Lanner falcons, Cape Vultures *Gyps coprotheres* and Black Storks *Ciconia nigra* were all present at the same site. Usually Lanner falcons will vigorously defend their nest against Black Eagles but sometimes Black Eagles elicit no reaction from Lanner falcons, despite being only a few metres from the nest (Gilmour 2003). In one transect of around 25 kilometres along the Ghaap Plateau escarpment in South Africa a flight survey detected seven territories of Common Kestrel, one Verreaux's Eagle, one Booted Eagle *Hieraaetus pennatus* and one Lanner falcon (Anderson and Hohne 2007). At a site in South Africa, Black Eagles tend to occupy their chosen nest site in May or earlier, and the Lanner falcons are forced to use an alternative nest site that is not in use, so that if a nest was repaired by a Black Eagle then the Lanner falcons had to use the cliff ledge (Craib 1977). Nevertheless, before the breeding season Lanner falcons can become aggressive and can be successful in driving off Black Eagle and Jackal Buzzard *Buteo rufofuscus* (Craib 1977).

In area of four thousand square kilometres in Central Southern Sicily, Egyptian Vulture *Neophron percnopterus* have been observed on many occasions near the nest of Lanner falcons with no reaction by the nesting birds (Mebs 1959, Salvo 1984). Nevertheless in Greece, the Egyptian Vulture seems to be affected by competition with other raptors, including the Lanner falcon (Vlachos *et al.* 1998). At one site in North Eastern Greece the resident Egyptian Vulture has been known to desert nest sites due to direct competition from a pair of Lanner falcons. Salvo (1984) also reported the absence of any reaction by individuals of *F. b. feldeggii* towards either Golden Eagle (NND = 2 km), Bonelli's Eagle (NND = 3 km), or Red Kite *M. milvus* nesting in the same cliffs as the Lanner falcons. The opposite was the case in a study published by Ciaccio *et al.* (1989), where the Lanner falcon was seen to attack individuals of both Egyptian Vulture and Bonelli's Eagle. Another raptor species that is frequently attacked by the Lanner falcon in Sicily is the Common buzzard *Buteo buteo* that uses the same cliffs as nesting sites in between 20 and 50% of occasions (Salvo 1984, Ciaccio *et al.* 1989).

It seems that large raptors such as Harriers and the Short-toed Eagle *Circaetus gallicus* are often attacked and driven off the territory of Lanner falcons (Dresser 1871-1881). An aggressive pair in Zimbabwe were observed attacking an African Fish Eagle *Haliaeetus vocifer* which was forced to roll over on its back and present its talons towards its aggressors (Barry 2004 b). In another interaction, a Bat Hawk *Macheiramphus alcinus* was circling at about sixty metres when it was attacked by a stoop from a Lanner Falcon which also called loudly against the intruder (Thomsett 1981). In Sicily, a very vigorous attack against a large eagle-like bird from a female Lanner falcon started loudly when the intruder was at least 1.5 km from the nest and it was pursued by numerous stooping flights against it for around 3.5 km (Stig F. Olsen pers. comm.).

One notable relationship has been observed to occur between the Lanner falcon and the Bateleur *Terathopius ecaudatus* which involves the re-use of breeding sites. In a nest in Zimbabwe, after the disappearance of the egg of a Bateleur pair, the Lanner falcon took over the nest and reared a brood (Steyn 1980). Another Bateleur nest was used by a pair of Lanner falcons after the nestlings flew but the Bateleur nestling was persistently worried by the falcons during its last week in the nest, and they took over as soon as it flew (Steyn 1980). Such interactions may be more than coincidence as the Bateleur lays early in the season and has normally raised its chicks by July or August, around the same time when Lanner falcons usually lay their eggs, so this instance of nest site re-use may well be more common (Steyn 1980).

Among nocturnal raptors, competition with Eurasian Eagle Owl *Bubo bubo* for nesting sites has also been observed. For example, one site was occupied by *F. b. feldeggii* due to the shooting of a pair of owls, and another pair of Lanner falcons were able to establish a territory when owls were forced to leave the site due to disturbance (Chiavetta 1982). The NND with the Eurasian Eagle Owl in Emilia-Romagna in Northern Italy is 4.5 km but in practice is probably less than 1-2 km (Chiavetta 1982). Generally, strong reactions are observed by adult Lanner falcon parents against large owls especially (Sharpe 1904).

Finally, one case of active defensive behaviour by a Lanner falcon against a Red fox *Vulpes vulpes* approaching fledged young in Sicily has been recorded (Ciaccio *et al.* 1989).

Other non-raptor species

Among other large birds, Ravens *Corvus* sp. have been observed many times interacting with Lanner falcons, especially during the breeding season (Figure 4.5; Mebs 1959) and in many cases they share the same nesting cliff. In a number of instances Raven *Corvus corax* have built their nest in abandoned Lanner falcon nests and vice-versa (Mascara 2006). In Sicily, co-occupancy of nest sites by both species ranged from 23 to 50% with nests separated by distances of between 50–60 m (Salvo 1984, Ciaccio *et al.* 1989, Mascara 2006). In Sicily and Calabria, distances between nests were much shorter at around 10-15 m but the site was characterised by continuous aggressive inter-specific interactions (Mirabelli 1982, Ciaccio *et al.* 1989). In most cases in the Eastern Cape of South Africa, Ravens had other nests which they would move to after the Lanner falcons had displaced them (Stephenson 2001). Lanner falcons breed up to a month earlier than Ravens and were more aggressive in defending their nests at the onset of egg laying (Stephenson 2001). In one case when Ravens did not have an alternative nest site and waited until the Lanner falcon chicks had fledged before they bred successfully (Stephenson 2001). Aggressive behaviours have also been reported between both adults and young Lanner falcons towards White-necked Ravens *C. albicollis* and Black Crows *C. capensis* (Sharpe 1904, Kemp

Figure 4.5 An aggressive display by an adult Lanner falcon *F. b. feldeggii* against a Raven *Corvus corax*, a situation frequently observed during the breeding season. © and courtesy by Marco Preziosi.

1993) and in Ghana an individual of *F. b. abyssinicus* attacked a Pied Crow (Dowsett-Lemaire and Dowsett 2014).

Overall however, relationships with other species of large birds were for the most part non-aggressive and, for example, the Lanner falcon may use an old nest on the same pylon or the same cliff as Black Stork *Ciconia nigra* (Brown *et al.* 1982). In addition, all Lanner falcon races regularly re-use old or abandoned nests of several bird species across all of their distributional area (see Chapter 6). One exception, reported by Sauer (1969), was of very aggressive displays by South African Ostrich (*Struthio camelus*) towards a Lanner Falcon which was trying to predate its chicks.

Peregrine and other large falcons

The historical biogeography and the current distribution patterns of both species suggest many possible contacts between Lanner and Saker falcons (see Chapter 3). The Balkans, and especially Bulgaria, seem to be a region where hybridization could possibly occur due to the overlap in the distributional ranges of the species (Iankov 2007). Contact between Lanner and Saker falcons could also be possible in Sicily where the wintering areas of two tracked Saker falcons were located in a large area surrounded at least by ten Lanner falcon territories (M. Prommer pers. comm., Bondì *et al.* 2014). In another wintering area in Ethiopia, a single Saker falcon was seen being harassed by a pair of Lanner Falcons while it was on passage to the Bale Mountains National Park. Turkey is another possible contact zone but there are currently no records regarding possible interactions in that country.

The Lanner falcon could be in competition with the Barbary falcon *F. p. pelegrinoides* in several areas in North Africa and the Middle East. It is possible that habitat segregation separates these large falcons and in Algeria the Lanner is more common than the Barbary falcon in the desert zones and in northern regions, although it is less attracted to areas of sea cliffs which are more favoured by the Barbary falcon (Ledant *et al.* 1981). In the Ouarsenis mountains of north-western Algeria, eight breeding pairs of Lanner falcons are found, while there are twenty-four pairs of Peregrine and Barbary falcons (Ledant *et al.* 1981). The Barbary falcon is also the dominant large falcon in central Arabia, probably due to its use of safe high cliffs, which are less favoured by the Lanner falcon (Jennings 1980).

Relationships between Lanner and Peregrine falcons are more complicated and it is not easy to quantify any possible effects of inter-species interactions on breeding performance and abundance (see Jenkins and Hockey 2001). In addition, the Lanner falcon is faced with a number of well-differentiated subspecies of the Peregrine that show a great deal of morphological variation, such as the Mediterranean *F. p. brookei* and the southern African *F. p. minor*, which could lead to different results from competition between the various subspecies and races. For instance, an apparent dominance of the Peregrine species over *F. b. feldeggii* is reported in Mediterranean Europe, while *F. b. biarmicus* largely dominates in southern Africa to the detriment *F. p. minor* (Jenkins and Hockey 2001, Andreotti *et al.* 2008).

Several studies have tried to untangle overlapping habitat requirements, choice of nesting sites, and territory size in different parts of the distributional areas. In one early study in Sicily, the Lanner falcon occupied 17% of the available territories as opposed to 29% by Peregrines, and in only 14% of cases were both species found to occur together in the same place (Siracusa *et al.* 1991). Most papers tend to oversimplify these complexities by referring to direct replacement of one species by another, or to local dominance of a single species. For instance in Kenya, the Lanner falcon is more common than the Peregrine and, while these two large falcons occur in different habitats, the Lanner may exclude the Peregrine perhaps explaining why in some areas only one occurs (Lewis and Pomeroy 1989).

In Zimbabwe, slightly less than 20% of Peregrine sites were re-occupied by the Lanner falcon especially those in deforested zones (Hartley 2000). On the other hand, it seems that in some parts of the Italian mainland especially, dominant Peregrines are in the process of usurping Lanner falcon nesting sites (Pellegrini *et al.* 1993, Martelli and Rigacci 2001, M. Brunelli pers. comm.). Nevertheless, a dynamic equilibrium between these two falcons is the most likely explanation for these phenomenon because local extinctions would more likely be attributable to the intrinsic attributes of each of the individual species rather than solely to direct competition between them. Recent research has therefore focussed mainly on searching for specific differences between the Lanner and the Peregrine falcons in attempting to explain relative abundance and rarity (Jenkins and Hockey 2001).

Overall habitat needs seem to be one of the most important factors in segregating

Subspecies	Location	NND (m)	Most abundant species
F. b. feldeggii	Sibillini Mountains (Central Apennines)	4000	P
F. b. biarmicus	Lukenya hills (Kenya)	80	L
F. b. feldeggii	Central Southern Sicily	2500	P
F. b. feldeggii	Central Eastern Sicily	1500	P
F. b. feldeggii	Central Apennines (Central Italy)	3300	P
F. b. feldeggii	Calabria (Southern Italy)	1500	P
F. b. feldeggii	Emilian Apennines	90–6000	P
F. b. feldeggii	Latium (Central Italy)	3300	P

Table 4.1 Nearest Neighbour Distance (NND) between active nests of Lanner and Peregrine falcons in relation to the relative dominance measured as field abundance (Chiavetta 1982, Mirabelli 1982, Salvo 1984, Ciaccio *et al.* 1989, Magrini and Armentano 1994, Manzi and Perna 1994, Brunelli and Sarrocco 2013).

these species. At a landscape level for instance, to the south of the 34th parallel in Tunisia the Lanner falcon almost completely replaces the Peregrine (Azafzaf 1999). In the past, some segregation occurred at coastal areas in Morocco with wooded areas and coastal cliffs used by Peregrines but largely avoided by the Lanner falcon (Heim de Balsac and Mayaud 1962). In Zimbabwe the Lanner falcon is more widespread and common than the Peregrine and does not seem to be subject to the same ecological limitations (Irwin 1981). In Eastern Africa, the two species generally occupy different habitats, with Lanner falcons found mainly in grasslands (with or without rocky hills) and in bushy or wooded areas, whereas the Peregrine is only found in close association with mountains and high cliffs (Britton 1980). The Lanner falcon is not confined to areas with cliffs as the Peregrine is, but can breed in open woodland wherever nests of other raptors or crows are available (Brown *et al.* 1982). Overall in East Africa, the Lanner falcon may be capable of excluding the smaller Peregrine in areas where both make their nests on cliffs (Britton 1980). In Guinea, over a total of 3635 km of road surveys, twenty-eight Lanner falcons were encountered but only two Peregrines (Rondeau *et al.* 2007). By contrast, areas that are largely unfavourable for the Lanner falcon, such as the Sibillini Mountains, greatly limited its abundance (0-1 breeding pairs; Manzi and Perna 1994).

Habitat level quantitative analysis carried out on the characteristics of nesting sites and their effects on breeding performance gave results different to those at landscape level. In Abruzzo in Central Italy the land use of thirteen Lanner nesting sites was not found to be any different from seven where it was replaced by Peregrine (De Sanctis *et al.* 2009). In Kenya, both falcons have nested at Njorowa Gorge (in the same nest hole in different years) and Eagle Hill (usually occupied by Peregrines; Britton 1980). In Sicily, Peregrines seems to select mainly calcareous cliffs whereas the Lanner falcon does not differentiate between different rock types and is equally likely to be found nesting on cliffs of calcareous rock, conglomerate, sandstone, and gypsum (Siracusa *et al.* 1991). Studies by both Mirabelli (1982) and Ciaccio *et al.* (1989), came to the conclusion that differences in habitat preferences meant that inter-specific competition and aggression between these species of falcon was avoided in Sicily and Calabria.

Even though Lanner and Peregrine falcons have been known to successfully share the same breeding cliff, in such cases territorial displays between the two species are frequently observed, such as in the Lukenya hills of Kenya for example. The Lanner falcon may be at an advantage as it starts defending the sites approximately one month earlier than the Peregrine, as has been found in one study in Zimbabwe (Thomson 1984). Distances between active nests can vary greatly as can be seen from the figures listed in Table 4.1. In another study carried out in south-central Sicily, fourteen breeding pairs of Peregrine were found to be nesting close to Lanner falcon sites, but the Peregrines showed a preference for sites located on much higher cliffs (Salvo 1984). As shown in Figure 4.3 significant differences exist between the slope ratios of cliff sites favoured by the Lanner and Peregrine falcons in Sicily where only sub-optimal sites for the Lanner falcon overlapped with those of the Peregrines (Amato *et al.* 2014).

In many rocky areas of Zambia, the Lanner falcon replaces Peregrines and active confrontation between the two has been observed, to the detriment of the Peregrine (Dowsett *et al.* 2008). In Zimbabwe, a Lanner falcon pair with three chicks in the nest vigorously attacked and drove off an adult Peregrine approaching their nesting area (Barry 2004a). There have been similar reports from Morocco where interactions between Lanner (*F. b. erlangeri*) and Peregrine falcons have been interpreted as competition for nesting sites. In South Africa, Lanner falcons outnumber Peregrines by a factor of ten to one in most areas and occupy a breeding range several times larger (Thomson 1984, Jenkins 1995). Peregrine and Lanner falcons do not breed at the same time of year in Southern Africa (Steyn 1983).

In Emilia Romagna in Northern Italy, many interactions (as well as active fighting) were reported by within 200 m of each other (Chiavetta 1982). After some intense interactions between the two species, the Lanner falcons decided to breed on another cliff 8.5 km away (Chiavetta 1982). The same study reports some very aggressive interactions between the two species, including a description of a screaming female Peregrine tumbling down over 200 m after reacting against a pair of Lanner falcons, and of one recently-fledged Peregrine that was stooped upon by a male Lanner with extended talons (Chiavetta 1982). In a similar situation in Campania where the species were nesting in very close proximity, Peregrines attacked a male Lanner falcon and fledglings (Mancuso and Gatto 2014). In Dadia National Park in Greece no Lanner falcon breeding attempts were observed after 2002 (previously there had been 1-2 breeding pairs), possibly due to the inter-specific competition brought about due to an increase in the numbers of Peregrine falcon, which seems to have led to the local extinction of the Lanner falcon (Poirazidis *et al.* 2011). Finally, a female Peregrine was observed harrying an immature female Lanner falcon as the latter passed southwards over the Lake of Benghazi in Libya (Gaskell 2005).

Female Peregrine falcons were significantly different from female Lanners in 18 of the 24 morphological measurements compared except bill size, ulna length, tarsus length and aspect ratio. Male Peregrines were significantly different from male Lanners in 17 of the measurements compared except body mass, bill size, tarsus length and width and length of toe 1 (Jenkins 1995). Thus, Peregrine and Lanner falcons were significantly different in all of the flight performance parameters compared (Jenkins 1995). Choice of nest-cliff is one of the primary outcomes of these structural differences (Jenkins 1995, Amato *et al.* 2014). For example, in the more open habitats of Zimbabwe, primary sites (> 100 m) may still be used by Peregrines, secondary sites (50–100 m) could be used by either species, and tertiary sites only by Lanner falcons (<50 m; Thomson 1984).

However, there is a question as to whether the definition of '*primary*' and '*secondary*' site is equally applicable and valid for both species. Many studies have demonstrated that such overlapping between nesting sites is of a fairly limited extent and seems to be independent of field abundance. In studies from south-central Sicily for example, many substitutions have been recorded over time with Peregrines competing with Lanner falcons but these have been successful at only three sites out of a total of twenty-two (Salvo 1984). In another study, of a total of eleven sites, five were used by Peregrines only, four by Lanner only, and two by both species, and in one case both species sharing the same cliff (length 600 m and height 80-120 m) for three years (fledging: P0 L1; P0 L1; P3 L1) (Chiavetta 1982). Also, where the Lanner falcon is dominant, the overlap is limited such as in an area of South Africa where four Peregrine eyries are known compared to only two of Lanner falcons (Tarboton and Allan 1984).

4.5 Breeding densities and spatial patterns

The density of breeding pairs depends on many factors including availability of suitable cliffs, recruitment rates, and the abundance of competitors. Many studies have reported relative densities of Lanner falcons nesting in different habitats and conditions. However, many of these have only supplied data relating to nesting sites occupied at least once by Lanner falcons and often do not elaborate on the number of pairs that breed at the same time within a given sample area (Leonardi 2001).

For example, in a four year study period in eastern Sicily occupancy was very variable and only around half of the available nest-sites were occupied by active pairs each year (Amato *et al.* 2014). In fact, it seems that each pair can have from two to four alternative nest sites spaced from between 3 to 5.5 km inside their territory (Kemp 1993). Alternative nests sites in Emilia-Romagna in Northern Italy were located at a distance of around 4 km (Chiavetta 1982). In Abruzzi in Central Italy, pairs used different cliffs in the same territory resulting in difficulties in relocating pairs year on year (De Sanctis *et al.* 2009). In south-central Sicily, twenty-two sites were occupied at least once but only thirteen continuously, six with some degree of discontinuity, and three were shared with Peregrines (Salvo 2001). Table 4.2 shows the relative densities of the Lanner falcon recorded in different countries and locations.

In northern central Italy, where the Peregrine falcon is the dominant species, the availability of suitable nesting sites, in terms of terrain features, seems to be the main factor which determines the spatial patterns and local densities of the Lanner falcon (Angelini *et al.* 1993, Manzi and Perna 1994). In South Africa, two pairs nested at either end of a small isolated cliff separated by a breeding pair of Black Eagles *Aquila verreauxii* (Kemp 1993). A similar case was observed in the Judean Desert of Israel where a Lanner falcon nest site was located within one kilometre of a Bonelli's Eagle nest and also a Barbary falcon nest (E. Bartov pers. comm.).

Table 4.3 show NND (km) between pairs of Lanner falcons in different geographical contexts. Low site fidelity may be an indication of the poorer quality of available sites, especially due to a lack of cliffs and surrounding areas with favourable low slope values (Manzi and Perna 1994, Amato *et al.* 2014). For populations living at the periphery of the Italian part of the species distribution, occupancy of nest-sites fluctuates greatly over time, especially in Emilia-Romagna (Chiavetta and Martelli 1991). Thus, the populations of Marches, Umbria and Tuscany are representative of the northern demes, and are rather stable and probably connected to each other (Angelini *et al.* 1993). Similarly, in a study area near Pretoria, there was regular spacing between territories but the distances tended to vary annually due to the use of alternative sites (Kemp 1993). Tarboton and Allan (1984) reported higher densities of breeding pairs of Lanner Falcons (pairs spaced 2-5km apart) located in areas of continuous cliffs when compared to sites found in agricultural areas (pairs spaced 9-10 km apart), where the species appears to mainly breed in abandoned crows nests (Kemp 1993).

Higher pair densities should also be associated with greater prey availability. Heim de Balsac and Mayaud (1962) reported a high density of breeding pairs in Zemmour in north-western Morocco due to the abundance of the Bell's Dabb Lizard *Uromastyx acanthinura* which was the main prey species used to feed chicks. In Zimbabwe, a nest-site was located one kilometre from a river which was dry during the breeding season and where Lanner falcons could easily capture chickens raised by local resi-

Subspecies	Location	Study period	Density km^2/bp
F. b. feldeggii	Marches and Umbria, central Italy	1990s	1350–2700
F. b. erlangeri	Ouargla Oasis, Algeria	2008–2009	0.5–1
F. b. erlangeri	Haouz province, Morocco	1990s	331–441
F. b. tanypterus	Judean and Negev deserts, Israel	1980–1985	389
F. b. feldeggii	Sicily, Southern Italy	1981–1988	58–79
F. b. biarmicus	E Cape Province, South Africa	1997–2000	236
F. b. feldeggii	Gravine, Apulia, southern Italy	2004–2007	89
F. b. feldeggii	Calabria, southern Italy	1970s	437

Table 4.2 Densities of breeding pairs of Lanner falcon in different parts of the distributional area (Mirabelli 1982, Frumkin 1986, Siracusa *et al.* 1991, Angelini *et al.* 1994, Morimando *et al.* 1997, Barreau and Bergier 2001, Stephenson 2001, Laterza and Cillo 2008, Guezoul *et al.* 2013).

dents (Barbour 1971).

The wide and scattered distribution of *F. b. feldeggii* breeding sites suggest good interconnectivity between occupied cells, as predicted by the dynamic metapopulation model (Andreotti *et al.* 2008). New colonization processes toward suitable isolated cells may therefore be directly related to the different sizes of the clustered subpopulations surrounding them (Andreotti *et al.* 2008). Long-terms studies on the peripheral subpopulation in the northern Apennines suggest a process of continuous extinction–colonization, which disproportionately affects the smaller and more isolated clusters (Martelli and Rigacci 1991). On the other hand, the large subpopulation in Sicily is probably sustained by good numbers of pairs in contiguous cells balancing the high rate of nest failures of up to 45% at the early stages of reproduction (Andreotti *et al.* 2008).

Home range

How large is the typical foraging area of the Lanner falcon? Do differences in territory size exist between males and females as is the case with other large falcons? Surprisingly there are insufficient data to attempt to answer these questions. Unlike with Peregrine and Gyrfalcons, there is a lack of studies which make use of tagged birds to investigate behaviour for the Lanner falcon, even for the threatened *F. b. feldeggii* race. For this reason, any comments on the spatial use of territory can at this stage be merely speculative, although some studies do give some indicative figures. In Sicily, for example, Mebs (1959) proposed a hunting range radius of around 4

Subspecies	Location	NND (Km)
F. b. feldeggii	Calabria	4–40
F. b. biarmicus	Formerly Transvaal, South Africa	3.1–4
F. b. biarmicus	South Africa	0.15–0.25
F. b. biarmicus	Pretoria, South Africa	6.9 (0.2–10)
F. b. erlangeri	Eastern coastal Morocco	5
F. b. feldeggii	Central Southern Sicily	5
F. b. abyssinicus	Serir Tibesti (Chad)	14
F. b. feldeggii	Gargano, Apulia, Southern Italy	6
F. b. feldeggii	Sicily, Southern Italy	2
F. b. feldeggii	Central Apennines	15.9
F. b. biarmicus	Eastern Cape Province, South Africa	8.5–19.5–48
F. b. feldeggii	SPA Gravine, Apulia	8.6–14
F. b. feldeggii	Emilia-Romagna, Northern Italy	5.5–14
F. b. biarmicus	Zambia	1.8–13.5
F. b. biarmicus	Namibia	4
F. b. feldeggii	Central Italy	6
F. b. feldeggii	Latium (Central Italy)	27.3
F. b. biarmicus	Waterberg, Namibia	0.9- 4.0-10.1

Table 4.3 NND (km) between Lanner falcon pairs in different geographical contexts (Jany 1960, Brown *et al.* 1982, Chiavetta 1982, Mirabelli 1982, Salvo 1984, Bergier 1987, Brown and Cooper 1987, Ciaccio *et al.* 1989, Bassi *et al.* 1992, Kemp 1993, Magrini and Armentano 1994, Talamo 1998, Stephenson 2001, Laterza and Cillo 2008, Brunelli and Sarrocco 2013).

km from the nest site, including a preferred perch site where parents start hunting flights towards open habitats. Chiavetta (1982) recorded a territory radius of 5 km in Emilia-Romagna in northern Italy. In South Africa, Jenkins (1995) observed Lanner falcons hunting up to 10 km away from the nest site. He first made an accurate estimation of the area around the nest site (Jenkins 1995) and using these figures he observed that the home range of two Peregrine pairs (0.85 km^2 and 0.81 km^2) were smaller than those of two Lanner falcon pairs (1.29 km^2 and 1.13 km^2; Jenkins 1995). Table 4.4 lists the approximate sizes of territories used by the Lanner falcon in different geographical contexts.

The sole study involving radio-tracked individuals was made in the Eastern Cape province of South Africa using three adults (two males and one female) during the period when they were rearing young (Stephenson 2001). Males were trapped and fitted with transmitters once the females had begun incubation, in order to determine

Subspecies	Location	Territory size km^2
F. b. biarmicus	Transvaal, South Africa	40–50
F. b. biarmicus	Pretoria, South Africa	100
F. b. feldeggii	Sicily, southern Italy	68.7 (SD = 10.3)
F. b. feldeggii	Central southern Sicily, Italy	16
F. b. feldeggii	Gargano, Apulia, southern Italy	525
F. b. feldeggii	Central Italy	425–850
F. b. feldeggii	Mediterranean Europe	60.7
F. b. feldeggii	Central Appenines, Italy	450–643
F. b. erlangeri	Ouargla Oasis, Algeria	0.1
F. b. biarmicus	Masite and Qeme Plateau, Lesotho	10–20

Table 4.4 Approximate size of territories used by the Lanner falcon in different geographical contexts. These data were not obtained from tagged individuals (Brown *et al.* 1982, Salvo 1984, Siracusa *et al.* 1991, Magrini and Armentano 1994, Talamo 1998, Kopij 2010, Guezoul *et al.* 2013)

their foraging range during the breeding season (Stephenson 2001). The female was fitted with a transmitter only after the chicks were more than twenty days old and both parents were actively hunting for food (Stephenson 2001). Foraging areas used by the three birds were 66 km^2 (male), 249 km^2 (male) and 225 km^2 (female) (Stephenson 2001). More than 50% of the smaller foraging range of the first male consisted of open or cultivated land (mainly sunflower, birdseed, and chicory fields) where it preferentially hunted (Stephenson 2001), mostly by means of high-speed fights low over the ground surprising bird prey such as Rock pigeons and less Redeyed Doves (Stephenson 2001).

The tracked female travelled over much greater distances to forage (around 24 km) and to secure food for rearing chicks. The choice of hunting habitat was mainly Karoo veld and Acacia karoo trees in the area surrounding the nest site (Stephenson 2001). The female bird followed a the same habitual route every day, visiting farmhouses where it preyed mostly on domestic chickens and occasionally other birds such as mousebirds and bulbuls (Stephenson 2001). The last male hunted mainly larks and other small birds over open grasslands (Stephenson 2001).

Chapter 5.
Breeding season

5.1 Breeding phenology

Qualitative analysis

One of the primary life-history traits of a species is the timing of reproduction that can have a direct influence on the number of offspring produced *per* breeding attempt (Newton 1979, Svensson 1997). The choice of when to breed is therefore critical and individuals that breed later in the breeding season typically produce smaller broods or have offspring of lower quality (Newton 1979, Svensson 1997).

Although many ornithological handbooks mention the relative timings of different reproductive stages for the Lanner falcon, there have been very few quantitative studies that provide more detailed data. Figure 5.2 shows the approximate timings of egg deposition by the Lanner falcon in different countries compiled from all of the qualitative data available in extant published sources. As is to be expected, laying dates greatly differ between the Palearctic, where they are primarily driven by ambient

Figure 5.1 Copulation between a pair of Lanner falcon (*F. b. biarmicus*) Kgalagadi Tansfrontier Park; © and courtesy of Mohammed and Sharifa Jinnah.

FIGURE 5.2 Approximate dates of egg deposition by the Lanner falcon in different countries (H. Azafzaf pers. comm., Tristam 1865, Mebs 1959, Jany 1960, Thiollay 1978, Jennings 1980, Brown *et al.* 1982, Elgood 1982, MacLean 1984, Nikolaus 1987, Yosef 1988, Ciaccio *et al.* 1989, Penry 1994, Caldarella *et al.* 2005, Salewski and Martignoli 2005, Ash and Atkins 2009, Manvell 2010).

temperature, and the Afro-tropics where they are driven by the alternation between wet and dry seasons (Figure 5.2; Newton 1979).

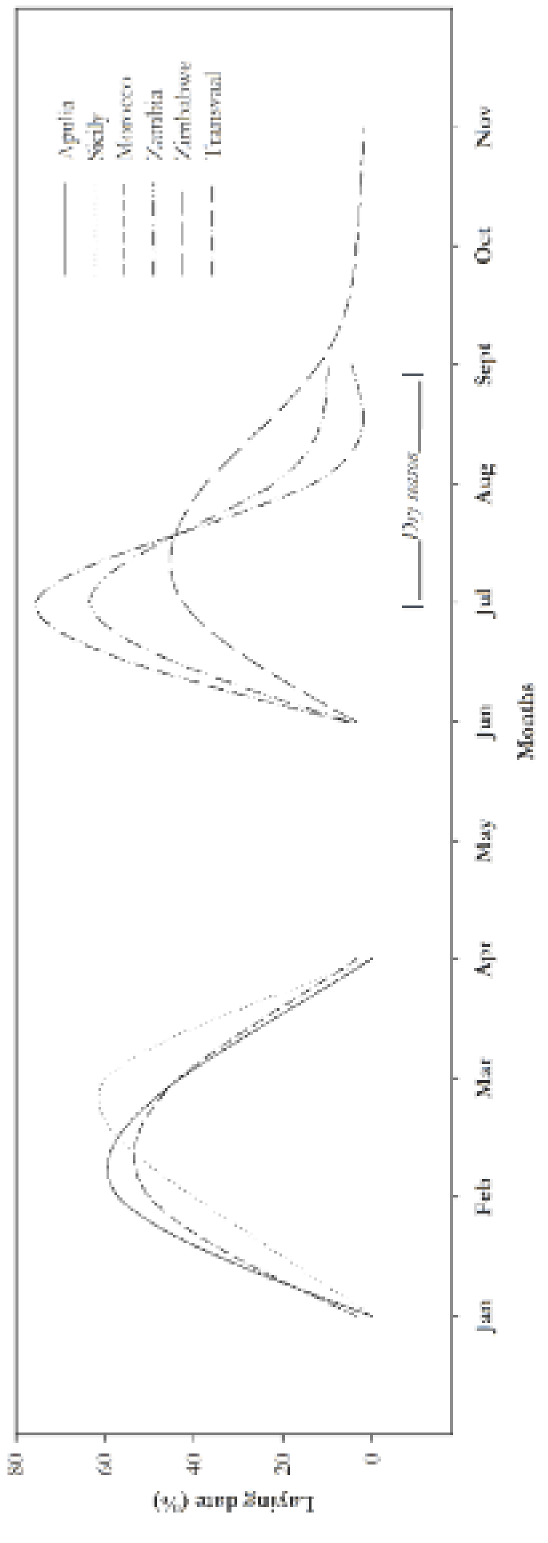
In tropical and southern Africa, the Lanner falcon breeds in areas where the most rainfall occurs during the summer, except in Somalia and Ethiopia where it may breed during the rainy season (Brown *et al.* 1982). Thus, egg-laying tends to occur in late winter to early spring and generally coincides with the dry season, although occasionally extending into wet periods (Craib 1977, Brown *et al.* 1982). Along the

Saharan belt the breeding season coincides with the onset of the spring migration of passerines, and egg deposition occurs mainly in February (Eastern Desert, Egypt) and March (Western Sahara and southern Algeria) (Figure 5.2). In Chad, Newby (1979) considered the Lanner falcon to be a cold season breeder. Breeding pairs (*F. b. tanypterus*) settled in the Taiz area of Yemen at the end of December and in central-southern Sicily (*F. b. feldeggii*) in January (Salvo 1984, Leonardi *et al.* 1992). In Morocco (*F. b. erlangeri*), breeding starts at the end of February with pairs settled in the Atlas Mountains in mid-March (Bergier 1987). In north and central Darfur, western Kordofan, and the Northern State of Sudan (ancient '*Nubia*'), breeding occurs in spring (Lynes 1925). In South Africa, where, as mentioned above, the Lanner falcon is a winter breeder, pairs occupy their nest sites in July (Craib 1977). A very peculiar situation occurred in Iran where the Lanner falcon (*F. b. feldeggii?*) seems to be a occasional summer breeder at Urmia Lake in the north-western region (Scott 2008). It may therefore be possible that longitude has an effect on laying dates but further investigation is necessary. Several cases of egg-laying outside the usual periods were recorded in different parts of the distributional area. Exceptionally, a pair with three young in flight was observed on 10 April in Gargano (Apulia) and these eggs were probably laid in the second half of January (Caldarella *et al.* 2005). On the other hand, a very late clutch was recorded in 1997 with two ten-day old chicks present at the end of May (Caldarella *et al.* 2005). In Sicily, one case was recorded of fledglings on the nest on 8 May, and nearby three twenty-day old chicks fledged between 21–28 May (Ciaccio *et al.* 1989). In Inner Anatolia in Turkey a nest was found to contain a chick in early May with egg laying having therefore taken place in early April (Kirwan *et al.* 2008). Overall, the Lanner falcon is considered a shy and elusive species and locating nests in the field is not easy during the breeding season. For instance, up until 1985 only one out of of fifteen breeding pairs was detected in Tuscany (Leonardi *et al.* 1992, Leonardi 2001). In addition, the Lanner falcon is less vociferous than the Peregrine during breeding leading to a reduced likelihood of detecting nests (Ciaccio *et al.* 1989, Leonardi *et al.* 2013).

Finally, in several studies many '*new*' breeding sites were discovered due to the misidentification of all the available sites within a territory and the tendency for birds to move between several of these alternative nest sites in consecutive seasons (Laterza and Cillo 2008, Leonardi *et al.* unpubl. data). Despite these difficulties, at most sites in Eastern Cape Province (as well as in Sicily) potential breeding could be confirmed after only an hour or two of observation once Lanner falcons were detected in craggy habitats (Stephenson 2001, Leonardi *et al.* unpubl. data).

Quantitative analysis

A study which made observations of breeding captive falcons of the nominate


Apulia
Sicily
Morocco
Zambia
Zimbabwe
Transvaal
Dry season
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov
Months
0
20
40
60
80
Laying date (%)

race *F. b. biarmicus* revealed which environmental stimuli have the most influence on the timing of reproduction. The birds were kept in captivity at a site in the United States of America and a two-year old captive female was seen to make a nesting scrape and begin to '*incubate*' this bare depression, as well as to cover bantam eggs, although she would not feed the hatched chicks (Snelling 1973). In September, the male spent some time scraping the artificial nest and in early February subtle changes in vocalizations were observed, followed by mutual responsiveness, and then copulation. During this study the photoperiod was just increasing following the winter solstice, which would be the equivalent to early August in the southern hemisphere, when wild Lanner falcons would normally begin courting (Snelling 1973). Photoperiod appears to be one of the main factors, along with food availability and habitat, that influences the onset of egg laying to a greater or lesser extent depending on geographic location (Sanz 1998, Greives *et al.* 2008).

Quantitative analysis shows some differences in laying dates between the Palearctic and Afro-tropical races (Figures 5.3 and 5.4). In Mediterranean Europe and North Africa, egg deposition is restricted to a short period from January to April with peaks in February and March (Figure 5.3). In Southern Africa, the peak laying times were in July and August during the dry season, although egg laying could be extended until as late as November (Figure 5.3). There appears to be a clear gradient effect of latitude on influencing egg deposition (Figure 5.4; Sanz 1998). It is probable that temperature and day length greatly affected the laying dates of the Palearctic races, as is the case for Common Kestrel, whereas in the southern hemisphere the abundance of prey during the dry season following heavy rains is more favourable for the egg production and the subsequent rearing of young (Figure 5.3; Carrillo and Gonzáles-Davila 2009).

5.2 Mating behaviour

When are Lanner falcons mature enough to mate and reproduce? Snelling (1973) suggests a minimum age of four years old but in captivity he successfully bred a female of three and a half years and a male of two and a half years. The complete development of gonads is clearly also a fundamental step. An adult *F. b. tanypterus* female in Egypt showed the prerequisite fat reserves, and an ovary of 27 × 14 mm with the largest follicle of 8 mm (Goodmam and Abdel Mowla Atta 1987). On dissection two small testes were found in a male *F. b. biarmicus* (Mundy and Hartley 2002), although another *juvenile* bird was also presumed to be a male but no gonads

FIGURE 5.3 Laying dates of the Lanner falcon in different countries measured as percentage frequency (%; $n = 277$ nests) (Mebs 1959, Benson *et al.* 1971, Irwin 1981, Bergier 1987, Tarboton and Allan 1984, Kemp 1993, Dean 2000, Dowsett *et al.* 2008, Laterza and Cillo 2008).

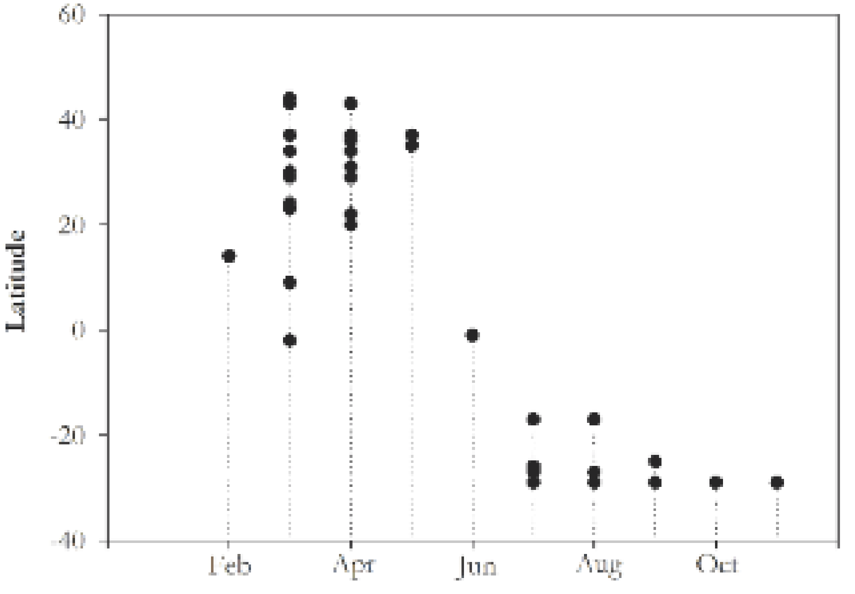


Figure 5.4 Laying dates and latitudinal gradients (*n* = 52 nests) (Warthausen 1860, Cochrane 1864, Tristam 1865, Layard and Sharpe 1875, Cavendish Taylor 1878, Giglioli 1889, Irby 1895, Erlanger 1898, Ogilvie-Grant 1902, Butler 1905, Raw *et al.* 1921, Lynes 1925, Wedgwood Bowen 1926, Guichard 1950, Coltart 1952, Stanford 1954, Jany 1960, Heim de Balsac and Mayaud 1962, Kellow-Webb and Dingley 1972, Chiavetta and Bonora 1973, Elgood *et al.* 1973, Snelling 1973, Mann 1976, Jennings 1980, Newby 1981, Chiavetta 1982, Snelling *et al.* 1984, Brooks *et al.* 1987, Yosef 1988, McGowan and Massa 1990, Morimando *et al.* 1997, Isenmann and Moali 2000, Barreau and Bergier 2001, Allan and McInnes 2002, Deacon *et al.* 2002, Gilmour 2003, Barry 2004a,b, Salewski and Martignoli 2005, Dowsett-Lemaire 2006, Kirwan *et al.* 2008, Grubac and Velevski 2010, Manvell 2010, Pavia *et al.* 2012, Bergier *et al.* 2013, Dowsett-Lemaire and Dowsett 2014).

could be found (Mundy and Hartley 2002). Courtship periods are between April and June in South Africa, mid-April in Gebel Elba in Egypt, late March at Wadi Aukau in south-eastern Egypt, early February in Calabria in southern Italy, and from December onwards in Emilia-Romagna in Northern Italy (Chiavetta 1982, Mirabelli 1982, Kemp 1993). The male probably selects the nest-site and then subsequently attracts a female to it (Brown *et al.* 1982).

Courtship displays consist mainly of mutual soaring and flapping flights with closely synchronized movements including mock attacks by either the male or female on its mate, leg-lowering by the male above its mate (and less often by the female), fast power-dives past one another, and wailing calls (Kemp 1993). In Zimbabwe, at the end of June partners were seen soaring and chasing each other near the nest site in spectacular aerial displays and were frequently observed performing food passing manoeuvres (Gilmour 2003). On the nesting cliff, the breeding pair often perch for long periods, screaming softly, or they may soar high together without aerobatics, screaming together. The female Lanner falcon is the dominant gender in the relationship, which has been confirmed in captive breeding attempts (Snelling 1973). The male feeds the female during mating displays, and also before she lays eggs (Figure s35; Brown *et al.* 1982). In one case, a male was seen to carry food 4.4 kilometres to feed the female near the future nest site (Kemp 1993). Copulation occurs near the nest site, either on the topmost branches of a tree or on a cliff ledge, and is recorded as having occurred even after the clutch has been laid (Figure 5.1; Dalling 1975, Sinclair and Walters 1976). Copulation was observed at Urmia Lake in Iran in mid-March (*F. b. feldeggii?*) but courtship displays were also observed as late as mid-August (Scott 2008). Courtship and copulation in *F. b. erlangeri* at Bir Moghrein in northern Mauritania was observed at the end of January (Bergier 1987). Copulation in *F. b. feldeggii* in south-central Sicily occurred between the middle and end of February (Salvo 1984). At Kgalagadi Transfrontier Park in South Africa a pair were seen to copulate in early August (M. Jinnah pers. comm.) and in Durban urban area in the first week of July (Sinclair and Walters 1976). In captivity, copulations occurred around ten days before the deposition of the first egg, once per day to assure fertilization during what would seem to have been a rather tenuous balancing act (Snelling 1973). The mutual bowing which preceded copulation was initiated by either bird and mounting usually lasted less than ten seconds, during which time both birds vocalised (Figure s36; Snelling 1973). The male balled up his feet prior to mounting and the female kept her head down and her tail cocked to the left (Figure 5.1; Snelling 1973). Overall, Lanner falcons are more subdued and less conspicuous in their mating displays when compared to the vigorous and loud displays of species such as the Gyrfalcon where males perform such elaborate behaviours as the curve-neck display (Wrege and Cade 1977). Nests of the Lanner falcon typically contain no material (Morimando *et al.* 1997). In fact, in common with other species of falcon, the Lanner falcon builds no actual nest structure itself. This could reveal a correlation between brain size and advanced cognitive abilities as the active transport of nesting material to the nesting site still takes place (Lefebvre *et al.* 2004). The relative brain mass of the Lanner falcon is 0.035 calculated as the unstandardised residuals of a linear regression analysis with body mass as the independent variable and brain volume as the dependent factor (Lefebvre *et al.* 2004).

Polyandry

It is reasonable to predict that Lanner falcons may quite often be cooperatively

Figure s35 A male *F. b. abyssinicus* feeds its larger mate on the Sanetti Plateau, in the Bale Mountains of Ethiopia. © and courtesy of Ignacio Yúfera.

Figure s36 A *F. b. biarmicus* pair perform courtship displays before copulation (South Africa). © and courtesy of Mohammed and Sharifa Jinnah.

polyandrous. In 1983, near Durban in South Africa, one adult male and a *juvenile* male were seen attending an eyrie with a single adult female *F. b. biarmicus* (Mendelsohn 1988).

5.3 Egg laying

The female Lanner falcon becomes quite lethargic a week before the deposition of the first egg and spends more and more time on the nest which is contained within a scrape around eight centimetres deep (Snelling 1973). Before the egg appears she raises her lower breast and abdomen feathers and begins pushing for around five minutes (Snelling 1973). Following laying, the female begins incubation immediately (Snelling 1973). Generally, eggs are laid at intervals of 2-3 days (Dalling 1975). For example, in a clutch of five eggs made in the window-box of a building in central Salisbury in Zimbabwe, the first egg was laid on the 19th July and the others following on the 21st, 25th, 28th and 29th (an average interval of 2.5 days; Kellow-Webb and Dingley 1972). In Durban city, the close inspection of the nest containing three eggs provoked attack from both parents, the male being more aggressive (Sinclair and Walters 1976). In a captive breeding attempt, the second egg was laid after three days, which is at least one day later than would be expected from a pair in the wild (Snelling 1973). In Zemmour in Northern Mauritania, as well as in similar Saharan desert zones, egg deposition is concentrated around the first week of March (Bergier 1987). In the Eastern Desert region of Egypt, the second egg arrived three days after the first was laid (Goodman and Haynes 1992). In southern-central Sicily, egg deposition has been recorded between the 17th and 19th of February (Salvo 1984). In Tuscany in northern Italy, egg deposition occurs at the end of March (Morimando *et al.* 1997) whereas egg laying in the Negev desert has been recorded as occurring in late February (Yosef 1988). In Emilia-Romagna in northern Italy, egg deposition generally takes place from the first week of March to early April, with the bulk of eggs being laid mainly in mid-March (Chiavetta 1982). Laying dates in the Palearctic ecozone depend largely on latitude with laying generally occurring earlier at lower latitudes and later at higher latitudes (Carrillo and Gonzáles-Davila 2009). In the southern hemisphere, the opposite seem to be case with egg laying at higher latitudes (nearer the equator) occurring much earlier than those at lower latitudes (Figure 5.3 and 5.4; Sebele 2012). Other factors that have been found to have an influence on the latitudinal variation in laying dates were temperature, rainfall, and photoperiod (Carrillo and Gonzáles-Davila 2009).

Clutch size

A comprehensive analysis that was carried out on Palearctic populations of breeding

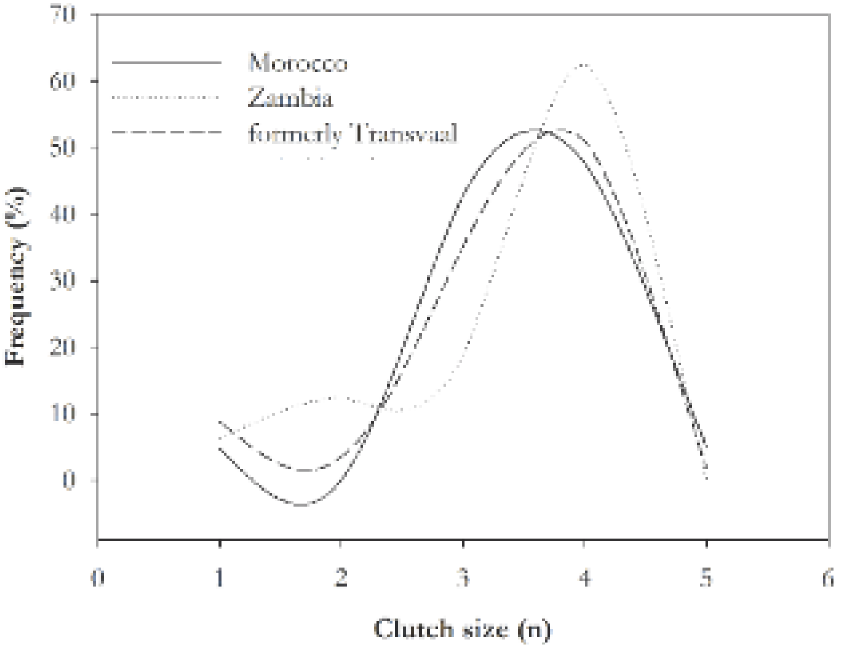


FIGURE 5.5 Frequencies of clutch size in Morocco, Zambia and the former Transvaal (now Gauteng, Limpopo, Mpumalanga, and the eastern part of North West Province). (Tarboton and Allan 1984, Bergier 1987, Dowsett *et al.* 2008).

Kestrels revealed a tendency for the clutch to increase in size towards northern latitudes (Carrillo and Gonzáles-Davila 2009). Unfortunately, testing whether this trend also holds true for the Lanner falcon is not feasible at the moment due to a lack of data for many countries. At a more local level it can be said that a slight difference occurred in mean clutch size between northern (2.9 eggs; range: 1-5) and southern (3.1; range 1-4) regions in Tunisia (T. Gaultier). In spite of this, the harsh environmental conditions experienced in these areas could well exert a greater influence on egg production than latitude, as has been seen to be the case for egg volumes (see Figure 2.33). The main range of clutch size when summarised by both race and location is between 3 and 4, which is as is to be expected from comparison with other falcon species (Figures 5.5 and 5.6). From a review of published sources, less than 20% of clutches consist of only one egg and many authors considered this as an incomplete clutch. By the same token, less than 10% of clutches have five eggs so this can be considered as the upper end of the scale (Figures 5.5). Trends for all races are quite similar with around 50% of clutches having four eggs except for *F. b. erlangeri* with a mean clutch size of three eggs (Figure 5.6). Differences by location are more likely to be linked with local environmental factors (Figure 5.5).

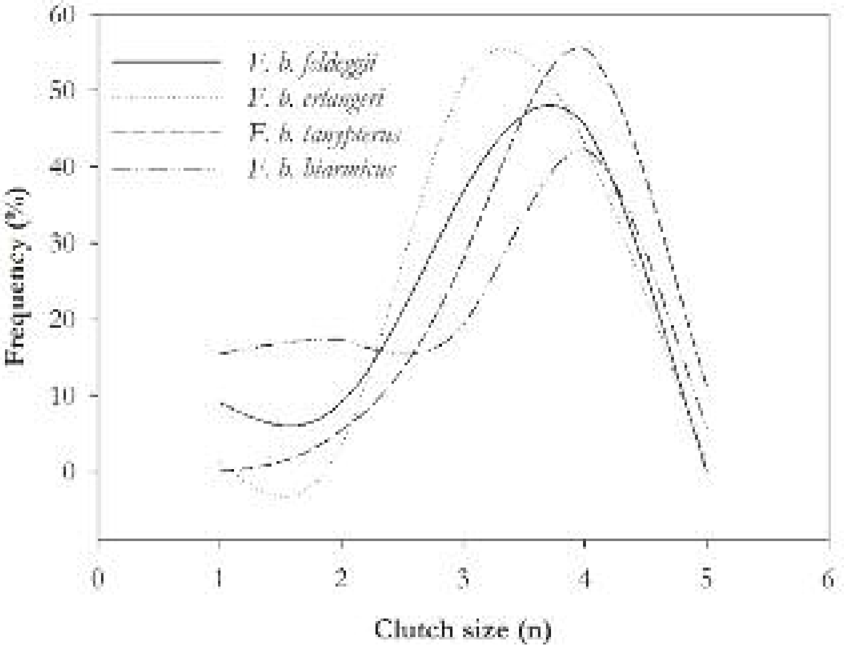


FIGURE 5.6 Frequencies of clutch size in each of the races of Lanner falcon (Warthausen 1860, Cochrane 1864, Tristam 1865, Cavendish Taylor 1878, Giglioli 1889, Irby 1895, Erlanger 1898, Ogilvie-Grant 1902, Whitaker 1905, Raw *et al.* 1921, Lynes 1925, Coltart 1952, Mebs 1959, Jany 1960, Schönwetter 1960, Heim de Balsac and Mayaud 1962, Kellow-Webb and Dingley 1972, Chiavetta and Bonora 1973, Newby 1981, Brown *et al.* 1982, MacLean 1984, Snelling *et al.* 1984, Bergier 1987, Yosef 1988, McGowan and Massa 1990, Goodman and Haynes 1992, Kemp 1993, Morimando *et al.* 1997, Isenmann and Moali 2000, Allan and McInnes 2002, Deacon *et al.* 2002, Gilmour 2003, Kirwan *et al.* 2008).

Although only three locations have exhaustive datasets, the overall trends are likely to remain the same due to the strong importance of physiological constraints on egg production (Troscianko 2014).

Double brooding

One case of double-brooding by *F. b. feldeggii* in Macedonia was recorded between 2002 and 2009 (Grubač and Velevski 2010). Another case of replacement was reported by Kemp (1993) where a pair incubating in mid-August had another clutch in late September, although both subsequently failed. In Israel where Lanner falcon eggs were collected for the purposes of reintroduction, a replacement clutch was laid in the same nest after the first clutch had been removed and five young hatched and fledged successfully from the nest (Hatzofe 2001). The only quantitative data gathered to date comes from the Transvaal region of South Africa, where a study has identified a percentage replacement of lost clutches of only 4.2% (Tarboton and Allan 1984). In one instance, once two successive clutches of four eggs had been taken the female laid a third clutch of three eggs in the same season, and on two further occasions females re-laid a clutch of four eggs after their first four-egg clutch had been taken (Tarboton and Allan 1984). A second clutch of three eggs was laid in Durban in the first week of October, one month after the nestlings first flight (Mendelsohn 1988). Probably second clutch is supported by high availability of prey in this urban area (Mendelsohn 1988).

5.4 Incubation

The incubation period varies slightly between countries and races from 28 to 35 days, with the average being 30-31 days (Brown *et al.* 1982). The nominate *F. b. biarmicus* has an incubation period of 32-42 days (32 days in Harare), while *F. b. feldeggii* has an incubation period of 32-35 days in Sicily, 28-30 in Calabria, and 28-30 in Emilia-Romagna (Chiavetta 1982, Mirabelli 1982, Steyn 1983, MacLean 1984, Ciaccio *et al.* 1989, Kemp 1993, Deacon *et al.* 2002). Nevertheless, it is possible for there to be some variation in the incubation period at the same nesting-site, such as at one site in Harare for example, where the incubation period was 40, 38, and 36 days in three consecutive years (Kellow-Webb and Dingley 1972).

When the complete clutch had been laid, both partners of a pair of *F. b. biarmicus*, were observed sitting continuously upon the eggs (Kellow-Webb and Dingley 1972, MacLean 1984). Conversely in Sicily, for the first 20 days only the female was seen brooding after which the male was observed on the nest but only for brief periods while the female was feeding or preening (Salvo 1984). In Apulia, the female did the bulk of the brooding, with the males only on the nest a few times, mainly some days before hatching (Laterza and Cillo 2008). In Calabria, incubation begins after the first or second egg has been laid, and is carried out by both sexes, the male often taking a fairly large share (up to 30% of daylight hours) but there is a large degree of variation between individuals. For the most part, males brood for not more than twenty-five minutes at a time, and the female makes use of this by sun- or dust-bathing (Mirabelli 1982). In most cases the male feeds the female on the nest but she may also be off the clutch long enough to kill her own prey. In Durban city, the male clucking loudly, female brought kill to nest and male still clucking loudly and seen feeding chicks (Sinclair and Walters 1976). The female sits alone on the nest by night and incubates the clutch. During observations of very elusive pair in Tuscany, the male changed over with the female at dusk and the female stayed on the nest all night. After changeovers, the male spent at most one hour brooding before the female returned after which the male then hunted for two hours and brought prey back to the nest (Pezzo *et al.* 1995). In Apulia, interruptions in incubation occurred at the middle and end of April and in one case the female continued brooding three weeks after the presumed hatching date (Laterza and Cillo 2008).

5.5 Egg hatching

Hatching is also a critical phase during breeding for the Lanner falcon (see Chapter 9). The whole hatching process in captivity takes about forty-eight hours and begins when the embryo breaks through the inner shell membrane to the air space and first vocalises (Snelling 1973). Eggs hatch over much shorter periods than laying, usually between 3 and 4 days, indicating that incubation of the first-laid egg is complete. In south-central Sicily, egg hatching occurs between 28-30 March (Salvo 1984).

Unfortunately, few field data exist regarding unhatched eggs but a consistent number of breeding failures could be attributable to this trait. For example, in the arid zones of Israel, in a clutch of four eggs there was one unhatched (Yosef 1988). In a nest in central Harare in Zimbabwe, two of a clutch of five eggs remained unhatched (Kellow-Webb and Dingley 1972). In Tuscany, in a clutch of two eggs one remained unhatched at the end of April (Pezzo *et al.* 1995). In a study at Apulia, adverse weather conditions may have had a negative impact on the proportion of unhatched eggs in the nest observed there with many cold and rainy days in the first half of March appearing to have an effect (Laterza and Cillo 2008). In western-central Sicily in 1958, of eighteen eggs laid in five clutches, 22% were unhatched which was assumed to be due to the very wet and cold weather earlier in the year (Mebs 1959).

5.6 Nestlings

The nestling period of *F. b. biarmicus* ranged from 38 to 47 days but was usually 42–45 or 44-46 days (Steyn 1983, MacLean 1984, Kemp 1993). Nestlings of *F. b. feldeggii* stay at the nest for 35-40 days, 44-46 in Sicily, and 44 days in Tuscany (Chiavetta 1982, Ciaccio *et al.* 1989, Pezzo *et al.* 1995). Overall in Africa, Brown *et al.* (1982) reported a nestling period of between 33-43 days with most taking between 35-40 days. In an urban nest of *F. b. biarmicus* in Harare in Zimbabwe, of a brood of three consisting of two females and a male, the latter left the nest very early at the age of 38 days (Mundy and Hartley 2002).

The hatched Lanner falcon weighs between 25 and 110 grammes after the first week (Snelling 1973). When they are first hatched, the young are feeble, helpless, and require constant brooding. Newly hatched chicks have a small white egg tooth in the bill, and their eyes are closed. By the time they are three days old their eyes are open (Kemp 1975) and they are able to utter a '*cack*' call of alarm (Snelling 1973).

At four days old the tooth on the cutting edge of the upper mandible is still present (Kemp 1975). At ten days old the nictitating membrane is apparent, and is almost transparent (Kemp 1975). In *F. b. biarmicus* the first signs of feathers appear in the wings and tail after fourteen days, usually by mid-September, and has completed after thirty-three days, usually by late September (Kellow-Webb and Dingley 1972). Asynchrony in egg deposition creates differences between nestlings with the youngest sibling often still having traces of '*down*' feathers while their siblings have fully-developed feathers (Kellow-Webb and Dingley 1972). After twenty-two days they are able to move about the nest and seize food, and soon after they can feed themselves (Kemp 1975).

At sites in the Central Transvaal, chicks are nearly half-grown by the end of September or early October (Kemp 1972). At the end of April in Dindéfello Nature Reserve in Senegal, a cliff nest of the race *F. b. abyssinicus* contained three full-developed chicks (Fernandez-Garcia *et al.* 2013). In desert areas of Libya, half-grown

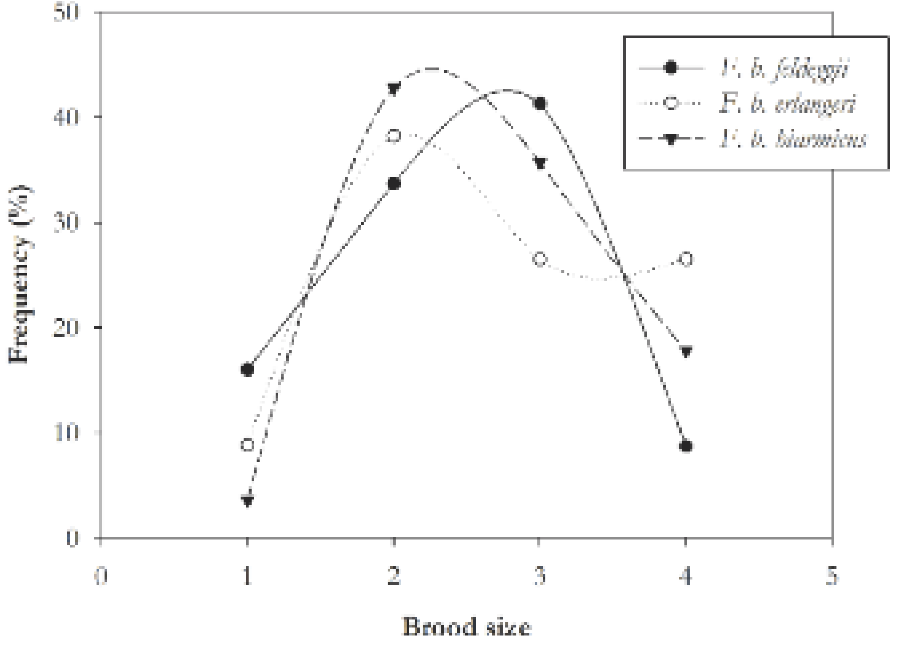


FIGURE 5.7 Frequencies of brood size in the various races of Lanner falcon (Layard and Sharpe 1875, Erlanger 1898, Orlando 1957, Mebs 1959, Jany 1960, Kellow-Webb and Dingley 1972, Chiavetta and Bonora 1973, Chiavetta 1982, Salvo 1984, Bergier 1987, McGowan and Massa 1990, Kemp 1993, Battista *et al.* 1995, Talamo 1998, Azafzaf 1999, Dean 2000, Barreau and Bergier 2001, Allan and McInnes 2002, Deacon *et al.* 2002, Gilmour 2003, Salewski and Martignoli 2005, De Sanctis *et al.* 2009, Grubac and Velevski 2010, Bergier *et al.* 2013, Mancuso and Gatto 2014).

chicks began to show sandy patches in the feathers on their heads and backs (Stanford 1954). Weight gain was rapid and fairly constant until peak weight was attained when 30 days old (Kemp 1975). The weight then declined until 55 days old, hereafter it levelled off at about 610 g, 14% below the peak weight of 710 g (Kemp 1975).

Apart from the actual day of hatching, mortality was highest in chicks during their first ten days of life but after that fewer deaths were observed (Stephenson 2001). In another case in Calabria, five chicks were hatched but only four fledged (Mirabelli 1982).

Brood size

The number of chicks inside a nest is obviously directly linked with clutch size as well as the crucial period of egg hatching (see *Productivity*). Several additional factors, including parental quality and available food resources, can greatly affect the chances of chicks surviving until fledging (see 5.8).

Long-term studies in different sample areas indicate a clear average brood size of 2-3 chicks, many fewer with four chicks (>10%), and a small portion with only

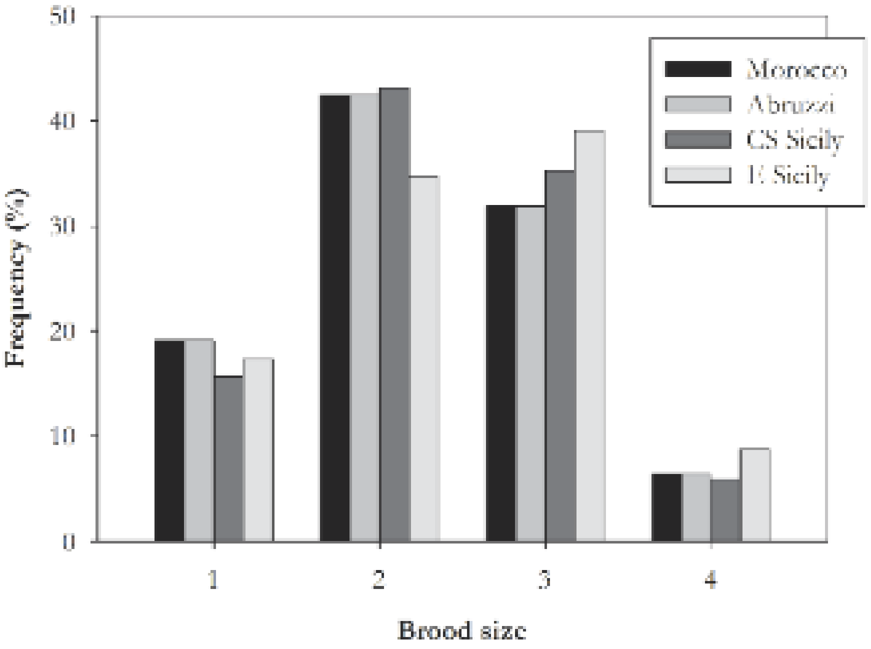


FIGURE 5.8 Frequencies of brood size in different intensively monitored sample areas (Morocco = *F. b. erlangeri*; Abruzzi, central southern Sicily, and eastern Sicily = *F. b. feldeggii*). (Bergier 1987, Ciaccio *et al.* 1989, Salvo 2001, De Sanctis *et al.* 2009).

	x ± SD	Nestlings	Fledgings	Sex ratio
Overall sample	38.2 ± 58.2	1.80	1.70	50.1
Re-occupied nesting sites	56.5 ± 85.7	2.40	2.10	63.0
Deserted nesting sites	25.3 ± 26.2	1.30	1.10	33.2

Table 5.1 Durations of vocal events made by male Lanner falcons (*F. b. feldeggii*) during the courtship period and mean numbers of nestlings and fledglings among re-occupied and deserted nesting sites in the following year (Leonardi *et al.* 2013). The sex ratio indicates the mean percentage proportion of males in the brood.

one (>20%; Figure 5.8). Data collected from various published sources confirm this tendency for 2–3 chicks with *F. b. erlangeri* and *F. b. biarmicus* showing a peak of two chicks and *F. b. feldeggii* a peak of three chicks (Figure 5.7). Exceptional broods of five chicks have been recorded for both *F. b. biarmicus* in southern Africa and *F. b. tanypterus* in Israel (Yosef 1988).

Sex ratio

As females are noticeably larger than males at an age of eight weeks it is possible for nestlings to be sexed quite early using leg length (Kellow-Webb and Dingley 1972). Female chicks also have larger feet and tarsi than males (Stephenson 2001). In fact, foot-span measurements of chicks older than twenty days show significant differences with the values for males averaging about 69 mm (69.1 ± 4.1; $n = 7$) and females around 76 mm (76.4 ± 4.4; n = 20; Stephenson 2001). Sex can also be made using DNA extraction from the CHD1 gene which is more reliable and accurate than morphological features (Figure 1.13; Brogna *et al.* 2005).

Lanner falcon pairs (*F. b. feldeggii*) which deserted breeding sites in the subsequent year tend to have been characterised by males performing shorter vocal events, and these sites have significantly fewer fledglings and fewer male offspring (Table 5.1). As has been the case with other studies, breeding pairs of Lanner falcon with vociferous males tend to have broods with more male offspring (Table 5.1; Leitner *et al.* 2006). In general, populations of raptors species which are characterised by reversed sexual dimorphism (RSD), as is the case with the Lanner falcon, larger eggs have been shown to produce male offspring (Anderson *et al.* 1997). In fact, females may manipulate the sex ratio of offspring and differentially allocate investment (such as yolk and testosterone levels) to produce males from larger eggs with higher growth rates and potential viability (Leitner *et al.* 2006).

In terms of sex ratio of brood, only scattered data exist, based for the most part on morphological features. These include a brood of three males and one female at Erkovit in Sudan (Wedgwood Bowen 1926), an urban nest in Harare in Zimbabwe with two females and one male (Kellow-Webb and Dingley 1972), a nest in the desert of Serir Tibesti in Libya with one female and one male, as well as study of broods in Pretoria with a small sample size, where the sex ratio was 0.5 (Kemp 1993). In Morocco, Bergier (1987) found a slight difference between the sex ratios of Mediterranean breeding pairs when compared to those from desert areas, where more females were produced in the desert as they were perhaps better able than males to survive the harsh conditions there.

5.7 Fledglings

Stretching and flapping activity by young Lanner falcons of the *F. b. feldeggii* race begins at around 20 days old (Figure s37; Salvo 1984). Generally, birds of *F. b. biarmicus* depart the nest helped by the female, the oldest leaving first while the youngest remain longest in the nest (Kellow-Webb and Dingley 1972).

Fledglings of *F. b. feldeggii* leave the nest on 8-11 May (Central Southern Sicily), 10-30 May (Calabria), mid-May-first week of June (Gargano), mainly in May (Eastern Sicily), early June (Tuscany), from the end of May to the end of June (Abruzzi), mid-May (Latium) and from 8 May to 6 Jun (mainly 15-25 May) in Emilia-Romagna (Chiavetta 1982, Mirabelli 1982, Salvo 1984, Ciaccio *et al.* 1989, Bassi *et al.* 1992, Pezzo *et al.* 1995, Talamo 1998, Caldarella *et al.* 2005, De Sanctis *et al.* 2009).

In the Lukenya hills of Kenya, newly fledged young of *F. b. biarmicus* were observed being fed on their cliff-based nest site in September. In the more arid areas of Israel, young fledged birds of *F. b. tanypterus* left the nest at the end of April and had completely left the breeding area by the beginning of June (Yosef 1988). At Lake Urumiyeh in Iran, an adult female and a sub-adult (*F. b. feldeggii?*) were observed in mid-March (Scott 2008) whereas young from an urban nest in Harare fledged in the first week of October (Kellow-Webb and Dingley 1972).

Productivity

The number of young fledged *per* successful pair is one of the most reliable dependent variables for evaluating the influence of limiting factors on breeding performance (Steenhof and Kochert 1982). The capacity of parents to successfully rear young to independence is therefore the first fundamental step for the persistence of a viable population in a territory. What are the rates of breeding failure in pairs of Lanner falcons and what are some of the likely types of causes? As a result of its status as a threatened subspecies, many of the studies that have been carried out to date have been concerned with *F. b. feldeggii* and few have focussed on gathering data for the other races (Leonardi *et al.* 1992). As a result, the available data are fragmented and incomplete, which means no clear trends so far have emerged for the

FIGURE S37 Stretching behaviour in *F. b. feldeggii* nestlings (Sicily, Italy). © and courtesy of Markus Varesvuo.

FIGURE S38 *F. b. tanypterus* fledgling perched near the nest (Judean desert, Israel). © and courtesy of Eyal Bartov.

Subspecies	Location	Fledgings/ attempts	Fledgings/ success
F. b. feldeggii	Macedonia	1.57 (n = 26)	Fled/success
F. b. erlangeri	Acqueduct Tunisa		2.15 (n = 19)
F. b. erlangeri	Morocco		2.5 (n =2)
F. b. feldeggii	Abruzzo (Italy)	2.08 (n = 51)	2.9 (n = 19)
F. b. feldeggii	Gargano, Apulia	2.08 (n = 19)	2.20 (?)
F. b. feldeggii	CS Sicily	1.83 (n = 12)	-
F. b. feldeggii	Molise		2.5–3 (range 2–4)
F. b. biarmicus	Pretoria, SA	1.3 (n = 31)	24 (n = 16)
F. b. tanypterus	Negev Desert	2.75 (n = 4)	3.7 (n = 3)
F. b. biarmicus	Transvaal	–	2.35 (n= 75)
F. b. biarmicus	South Africa	–	1.89 (n= 9)
F. b. feldeggii	Sicily	2.10 (n =?)	2.3 (n= ?)
F. b. feldeggii	CW Sicily	–	2.8

Table 5.2 Productivity of Lanner falcon pairs in different countries reported as ratios of fledglings/territorial pairs and fledglings/successful pairs (Mebs 1959, Brown *et al.* 1982, Salvo 1984, Tarboton and Allan 1984, Bergier 1987, Yosef 1988, Massa *et al.* 1991, Kemp 1993, Battista *et al.* 1995, Azafzaf 1999, Caldarella *et al.* 2005, De Sanctis *et al.* 2009, Grubac and Velevski 2010).

species as a whole (Table 5.2).

As stated by Brown *et al.* (1982), breeding success for the African populations of the Lanner falcon is generally good, with broods of 2-4 regularly reared, with a mean of 2.51 (fledging/pair successful; n = 47) (71% of mean clutch size) but, allowing for some failures and for the presence of some non-breeding pairs, the actual overall success may well be lower (see also *Brood size*). Brown *et al.* (1982) give a breeding failure percentage of 45-50% of the mean clutch size which is probably more accurate. The main methodological problem with this study was the lack of measurement of clutch size that does not allow for a comprehensive evaluation of pre- and post-hatching mortality (Leonardi *et al.* 1992).

From scattered field observations, egg infertility as a whole seems to be low as does mortality after the second week after hatching. Only one egg in forty-two was infertile in Morocco (Bergier 1987). In eastern Sicily, three chicks only a few days old and one *juvenile* bird were found dead, most probably predated by a Red Fox (Leonardi *et al.* unpubl. data).

In the Mediterranean regions of Morocco, Bergier (1987) assumed that rates of breeding success for pairs of Lanner falcon increase by up to four young fledged when compared to that of desert zones, due to the increased availability of prey.

	Central Southern Sicily			CE Sicily	Apulia	Harare	Emilia Romagna	Latium	formerly Transvaal	Southern Africa
	1978–1990 (n = 45)	1991–2000 (n = 25)	1981–1984 (n = 24)	1978–? (n = 70)	2004–2007	1997–2001 (n = 5)	1972–1981 (n = 17)	1988–1992 (n = 20)	1975–1981 (n = 96)	1970s (n = 9)
Deposition failures	2%	20%	0%	8%	10%	0%	12%	5%	-	-
Hatching failures	7%	30%	4%	14%	44%	0%	18%	16%	12%	-
Fledging failures	10%	0%	4%	12%	0%	10.5%	0%	25%	7%	-
Total failure	18%	44%	8%	27%	50%	10.5%	30%	46%	19%	47%
Fledging rate (fledged young/ successful pairs)	**2.30**	**2.36**	**2.40**	**2.31**	**2.80**	**3.40***	**2.20**	**2.60**	**2.35**	**1.89**

Nevertheless, long-term studies show that breeding success did not vary at sites such as Abruzzi in Central Italy during a period of almost three decades (De Sanctis *et al.* 2009). In the Transvaal region of South Africa, 84% of nesting attempts were successful, and a 75% where human interference is included (Tarboton and Allan 1984). In this case, causes of breeding failure included: eggs and chicks collected (44%), bad weather (17%), eggs deserted and chicks died (11%), predation (11%), as well as unknown causes (17%) (Tarboton and Allan 1984).

Figures for productivity and breeding failure have a strong strategic role to play in evaluating the health of threatened Lanner falcon populations (Andreotti and Leonardi 2007). It is therefore fundamental to collect these data in order to build up reliable measurements of conservation efforts. One of the most comprehensive studies on breeding biology of Lanner falcons was made by Salvo (2001) which covered more than twenty seasons in south-central Sicily (Table 5.3). Fledging rates during this long period remained largely consistent and very similar to those recorded at other locations (Tables 5.2 and 5.3). On the other hand, percentages of complete failures varied greatly between locations, especially in light of the different phases in the breeding cycle during which failures occurred (Table 5.3). Although insufficient data are available, a strong relationship exists (p <0.001) between deposition and hatching failures, although not with fledging rates (Figure 5.9). It is therefore plausible that there is a constant and significant contribution of factors relating to parental quality implicated in the causes of nesting failures, in spite of the roles played by local conditions and other stochastic factors.

5.8 Post- and non-breeding behaviours

In Algeria during the non-breeding period (July–February), birds occupied the open plains not far from their nesting sites (Ledant *et al.* 1981). A similar behavioural pattern was observed amongst breeding pairs and young on the Gargano peninsula and other regions of Apulia. Here, the birds congregated on the plains attracted by an abundance of prey species, particularly Orthopters such as locusts (M. Caldarella pers. comm., Laterza and Cillo 2008). A pair of Lanner falcons with three young have been observed in the Calabria National Park in southern Italy during July, hunting insects in the air above slopes and clearings (V. Škorpíková pers. comm.). Similarly, in Eastern Cape Province, adults and *juveniles* were observed in the summer months outside the breeding season foraging both on the ground and in the air with

Table 5.3 Percentages of the different causes of breeding failure and fledging rates between breeding seasons of Lanner falcon nesting attempts in different geographical areas (* = plus 18% mortality after fledging) (Brown *et al.* 1982, Chiavetta 1982, Salvo 1984, Tarboton and Allan 1984, Ciaccio *et al.* 1989, Bassi *et al.* 1992, Salvo 2001, Deacon *et al.* 2002, Laterza and Cillo 2008).

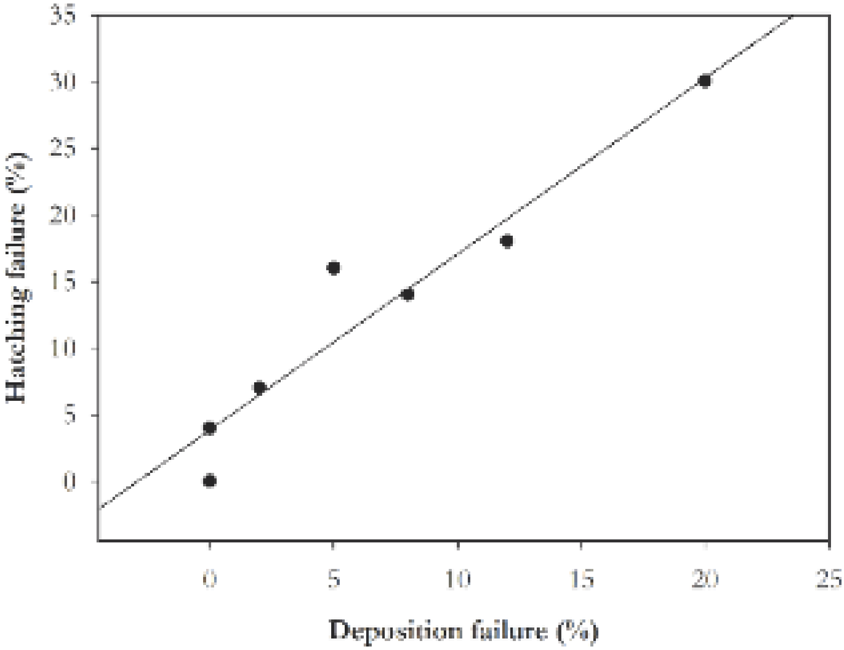


FIGURE 5.9 The significant relationship between egg deposition and hatching failures recorded in different Lanner falcon races and at different localities.

slow coursing flights, catching locusts and grasshoppers in areas of mown pastures and short grasslands as much as twenty kilometres away from the nest site (Stephenson 2001). The Lanner falcon has been known to opportunistically forage for desert locusts by following men and camels in northern Niger, and has been observed actively stooping on locusts that have been flushed. Birds have also been observed in south-eastern Niger feeding on grasshoppers (probably *Oedaleus senegalensis*) flushed by Abdim's Storks *Ciconia abdimii* (Jensen *et al.* 2008). In the Kalahari desert, groups of adult and *juvenile* Lanner falcons congregate at the end of the rainy season in June to feed on termites (J. Kruger pers. comm.; Figure 5.10). Groups of up to twenty Lanner falcons (*F. b. erlangeri*) have also been observed in Morocco, feeding and roosting in a desert area in order to exploit high local densities of *Psammomys obesus* (Laidi *et al.* 2012).

During the summer in south-central Sicily, between July and August, pairs continued to remain on their territories and make use of the nesting cliff for roosting and foraging (Salvo 1984). In the Gargano peninsula in Apulia, nest sites were visited all year round by owners although with increasing frequency from early December (Caldarella *et al.* 2005). Here, young birds (*F. b. biarmicus*) were regularly present on their territories in December, around ten weeks after fledging, and could be seen

Figure 5.10 A group of Lanner falcons (*F. b. biarmicus*) congregating at a temporary patch of water after the rains in the Kalahari. © and courtesy of Jannes Kruger.

receiving food from adults in talon-to-talon aerial passes (Dalling 1975, MacLean 1984, Kemp 1993). These young birds, at around 55-60 days old, may well be being trained in hunting methods by their parents (Caldarella *et al.* 2005). Similar behaviour has been observed in young birds being accompanied by their parents in Apoka in Kenya during the month of January (Carswell *et al.* 2005). In Sicily, young birds seem to stay with parents until September at the latest (Salvo 1984, Ciaccio *et al.* 1989).

Adults and young therefore remain very close for several weeks after fledging, with the young birds often being found in the vicinity of the nest and maintaining contact through a wide range of vocalizations. For example, a noisy meeting between adults and young has been observed at a nesting site even during the middle of August (Laterza and Cillo 2008). After one month of being taught by their parents, or around 20-25 days after fledging (although sometimes as much as 30-50 days), young birds are able to capture prey by themselves. Although there have been observations of apparent training of young birds continuing well into August (Chiavetta 1982, Mirabelli 1982), after the end of September, *juvenile* birds tend to leave their natal sites and there are only scattered observations of immature birds from locations far removed from the natal nesting areas (Laterza and Cillo 2008).

5.9 Parental care and investment

Generally, parental care is split between the sexes, with the female brooding and the male providing food (MacLean 1984, Salvo 1984). After the eggs have hatched, the female will often feed on prey before it is delivered to the chicks (Salvo 1984, Pezzo *et al.* 1995). For the first four days, the female broods chicks without pause and stays in the nest overnight in the first few weeks (Mebs 1959, Salvo 1984, Caldarella *et al.* 2005). The female broods or shades the chicks in the nest up until around day 10–14 and the male may also assist with brooding the young chicks during this period (Barbour 1971, Laterza and Cillo 2008). The male also begins to feed chicks after they are more than around thirteen days old (Brown *et al.* 1982).

Usually prey is passed between parents on favoured perching sites outside the nest (Barbour 1971, Salvo 1984). Similar behaviour has been observed in an urban environment, when chicks were only a few weeks old, the male hunted for prey that the female received from aerial passing or from a preferred perch site (Kellow-Webb and Dingley 1972). When feeding chicks, the female returns to the nest with the prey already de-feathered and beheaded, and chicks are encouraged to feed by a clucking vocalization (Kellow-Webb and Dingley 1972, Snelling 1973). Prey is usually distributed among the young by the female in this way for a month, and after that prey is delivered directly into the nest (Figure s39; Salvo 1984). In Tuscany, 27% of the prey that was delivered directly into the nest was mostly passed by males to females (73%) at favoured perching sites which were located on rock ledges and trees, although occasionally on bare ground (Figure s40; Pezzo *et al.* 1995). When chicks are 4–5 weeks old, the female feeds them at all times and the male is chased if he attempts to feed them (Figure 5.11; Kellow-Webb and Dingley 1972). If the male is delayed in returning with prey, the female may leave the nest and hunt herself, as has been observed in southern Africa, where a female left the nest and caught prey (such as domestic poultry) within five minutes (Barbour 1971).

The female remains constantly on the nest only during the period when the young are still very small and need to be covered, in a similar way to the Peregrine falcon, but, later, the eyrie is often completely unattended for hours because both parents are hunting cooperatively (Mebs 1959). In Sicily, males have a rock perch where they stay overnight which is usually close to the nest but may be up to two kilometres away (Mebs 1959). He usually arrived at the nest shortly after sunrise and stayed perched there with the female for some time (Mebs 1959). When the sun comes up it is therefore usually the male who begins the first hunt of the day (Mebs 1959).

Overall, the mean nest attendance of Lanner falcon parents (*F. b. biarmicus*) was 72.1% of the day, which is greater than that of the Peregrine (Jenkins 1992). Almost all of the brooding is carried out by the female except for brief pauses when she is hunting, when she is substituted by the male (Caldarella *et al.* 2005). In Abruzzi,

Figure s39 Female *F. b. feldeggii* parent bringing prey to 45-day old nestlings (Sicily, Italy). © and courtesy of Markus Varesvuo.

Figure s40 Food pass between a pair of *F. b. feldeggii* at a favourite perching site during the breeding season (Marches, Italy). © and courtesy of Bruno D'Amicis.

FIGURE 5.11 Female *F. b. erlangeri* feeding chicks with Bell's Dabb Lizard *Uromastyx acanthinura* © and courtesy of Marco Preziosi.

females left their eggs for more than forty-five minutes at a time, and sometimes over an hour (n = 6 – 48, 57, 60, 54, 63, 75), without resulting in any hatching failures (De Sanctis *et al.* 2009). In central Harare when chicks were 2–3 weeks old, the female started leaving the nest for short periods and during the subsequent week was away from the nest for up to ninety minutes (Kellow-Webb and Dingley 1972). Nevertheless, on these occasions the male would always be either on the nest or on a nearby perch-site (Figure s41; Kellow-Webb and Dingley 1972). One nesting site in Campania which was successful for three consecutive years failed during the fourth season due to the female leaving the eggs too many times for the absence of the mate (Mancuso and Gatto 2014). When the young are feathered, the female also starts to hunt, but generally remains near the nest for much of the time, even late into the fledging period (Brown *et al.* 1982). When the chicks are 10–20 days old, the female usually remains near the nest attacking other large birds and possible predators that threaten to come close, such as dogs, cats, and sometimes humans, but is generally less aggressive than the Peregrine in this regard (Brown *et al.* 1982). Parents will defend the young against intruders, preferring aerial attacks, and attempting to strike the intruder with a few glancing blows. The larger female tends to be more vigorous and persistent while the smaller male will stoop down on intruders but rarely making physical contact (Deacon *et al.* 2002).

Generally, the birds remain at a relatively large distance when humans are near the nest as has been observed during the intensive fieldwork for ringing nestlings in eastern Sicily (Leonardi *et al.* 2007). In another study in the desert area of Tibesti, when a nest with eggs was approached, the male flew very close to the eyrie and one parent circled the intruder and made several dives toward his head (Jany 1960). A pair of *F. b. biarmicus* mobbed an intruder at Bloemfontein in South Africa during September near a rocky cliff where the birds were probably nesting (Clarke 1904).

FIGURE s41 Adult male *F. b. feldeggii* (Sicily, Italy) always be either on the nest or on a nearby perch-site. © and courtesy of Markus Varesvuo.

FIGURE s42 Perched *juvenile F. b. feldeggii* (eastern Sicily, Italy) looks at its parents in flight . © and courtesy of Stig Frode Olsen.

Likewise, a breeding pair in Zimbabwe were very aggressive and the male struck the helmet of the researcher and both birds uttered '*kek-kek-kek-kek*' alarm calls (Gilmour 2003). However, there is some variation in the levels of aggression shown by birds, and, for example, a hide with a researcher inside was sited at less than five metres from the nest and was tolerated by the breeding pair after all of the eggs had hatched (Barbour 1971). During studies in Inner Anatolia, chicks were aggressive towards human intruders but adults tended to be more secretive and quiet (Kirwan *et al.* 2008).

Overall, males bring almost exclusively small items of prey such as small birds and mammals to the nest, while the female tends to bring larger prey items (Salvo 1984). Prey deliveries in Tuscany (average 1.5 per day; range 1–4) and average one prey item every two and a half hours (range 2–5 hours), mainly around mid-day and late afternoon (Figure 5.12; Pezzo *et al.* 1995). Nevertheless, a study with a large sample size demonstrates that the distribution of feeds does not differ significantly in relation to time of day (Jenkins 2000). In central southern Sicily, provisioning rates by males were 2–3 prey items per day (during the incubation period), one every 4.2 hours, and 3–4 prey per day, one every 3.5 hours (Salvo 1984). In Soutpansberg in northern South Africa, the rate was 7.44 prey per day (range 2–15), average 2.55 feeds per chick per day (range 0.75–4.00) (Jenkins 1992). The mean duration of feeds was 7.5 minutes (range 2.1–25.2 minutes) and the prey delivered consisted of 36% small, 52% medium-size, and 12% large items (Jenkins 1992). The number of prey brought to the nest decreased as the chicks grew older (Kellow-Webb and Dingley 1972). Finally, parents begin to bring live prey to the young birds (Kellow-Webb and Dingley 1972). Young birds, although they were autonomous and very bright, were always controlled by one of the parents perched near to the nest (Figure s42; Laterza and Cillo 2008).

The most in-depth analysis on parental care in the Lanner falcon was made by Jenkins (2000) using time-lapse photography at nine nests in Soutpansberg in the Northern Province of South Africa. As expected, feeding frequency was largely attributable to direct variation in brood size and nest attendance strongly decreased with the nestlings age (Jenkins 2000). Ambient temperature (both minimum and maximum) greatly affect the percentage amount of time spent brooding but had a positive effect on average feed interval (Jenkins 2000). It is unlikely that ambient temperatures had much effect on nestling energetics as these would be largely moderated by the brooding efforts of the parents (Jenkins 2000). In this study, the average number of feeds per day was 7.2±1.9, feeds per hour was 0.63±0.15. The average interval between feeds was 83±23 minutes and the average time per feed was 6.7±1.8 minutes (Jenkins 2000). The study found that the average size of prey delivered to the nest, and the incidence of medium to large prey in the diet, tended to increase with both brood size and age (Jenkins 2000). Interestingly, *juvenile* birds

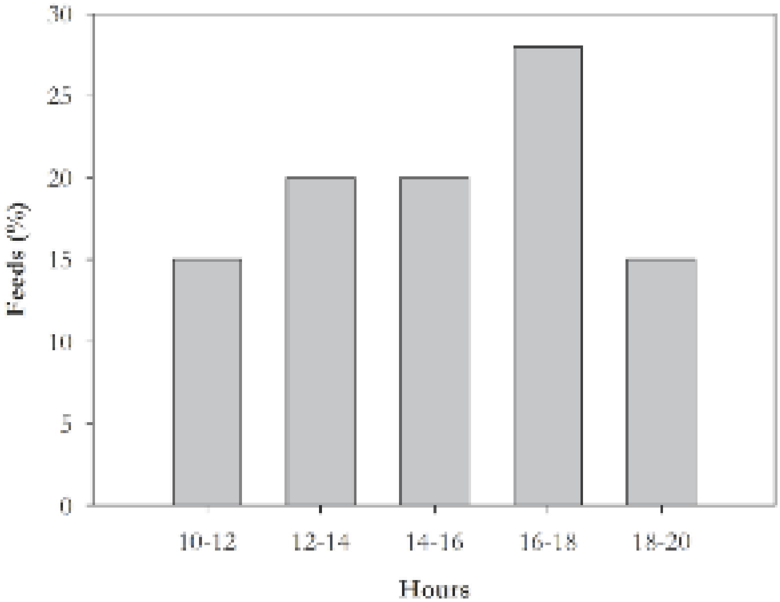


FIGURE 5.12 Percentage feeding frequencies of feeds delivered per day in Lanner falcon nests in Tuscany, northern Italy (Pezzo *et al.* 1995).

made up 46% of the diet of the Lanner falcon in Soutspanberg (Jenkins 2000).

5.10 Survival and recruitment

After fledging, young Lanner falcons are faced with several threats that decrease their chances of survival and the subsequent possibility of reaching reproductive age (see also 2.7). For instance, out of a total of fourteen individuals in Zimbabwe, three were found seriously injured and three (one immature male and two adult male and female) were found starving (Mundy and Hartley 2002). In another example, a *juvenile F. b. tanypterus* was found injured with a broken wing in Nahal Kziv in Israel about a month after its release in Ramat HaNadiv (Hatzofe 2001). Predation is another major factor that can affect survival, and the same Author found that three *juveniles* were predated shortly after their release by a pair of owls nesting close to their site at Nahal Hame'arot (Hatzofe 2001). The remains of a *juvenile F. b. feldeggii* that had been killed or run over was found in the nest of an Egyptian vulture in Macedonia (Grubac 1996). In an environment such as the city centre of Harare in Zimbabwe that is particularly dangerous for young birds, mortality after fledging from the nest was as high as 15% (Deacon *et al.* 2002). A ringed adult male that had bred twice at the same nest site died by collision (Stephenson 2001). Apart from the birds from Israel mentioned above, other tagged *juveniles* of *F. b. tanypterus* were recaptured in Saudi Arabia and Turkey very far from the natal site where they were originally tagged (Hatzofe 2001). Unfortunately, no other studies have been made using tagged individuals. In recent research in eastern Sicily, more than fifty *juveniles* were fitted with coloured plastic rings (white with black alphanumeric code) but without any subsequent recoveries (Cipriano 2005). A similar outcome resulted in a study in Eastern Cape Province, where no marked birds were re-trapped at different sites, and no adult falcons were recaptured away from their nest site (Stephenson 2001). Lanner falcons probably do not breed until they are at least three years old. Assuming an overall birth rate of 1.8 young per pair per year, and 75% mortality before sexual maturity, the average lifespan of an adult would be around four to five years (Brown *et al.* 1982). For example in Apulia in southern Italy, a pair bred successfully with a sub-adult female producing three chicks, and again in the second year when the pair was monitored the same female produced three chicks. However, in the third year only the male was present along with an immature female that had been present the year before and no breeding took place. In the fourth year of observations, the site was again occupied by an adult pair (possibly the same female as before) and the pair again produced a brood of three chicks (Laterza and Cillo 2008). Similarly in Eastern Cape Province, where a marked falcon disappeared at a breeding site and was replaced by a new mate, breeding success was invariably lower than had been recorded for pairs that had bred previously at the same site (Stephenson 2001). Newly-formed pairs also tended to have poorer fledging rates, with one study following a pair that had bred successfully for three years only producing one chick when the female was replaced at the start of a new season (Stephenson 2001). Between 1997–2000, out of a total of twelve adult falcons, six were replaced and of these two pairs failed to return to their breeding sites (Stephenson 2001). In another study in the Northern Apennines, a pair laid a single unhatched egg in their first year whereas the following year using another site on nearby cliffs they successfully raised three young (Chiavetta and Bonora 1973).In South Africa, a study recorded significant turnover of birds which was marked by the disappearance of a tagged male and by the recruitment of subadult birds into a breeding pair at least three times in four nest sites (Kemp 1993). In a similar situation in Calabria in southern Italy, substitution did not take place in the subsequent season but only after two years (Mirabelli 1982). In Eastern Cape Province, eight out of twenty-five breeding sites produced young, and several sites had single adult birds roosting on cliffs but with no attempts at breeding (Stephenson 2001). It is therefore possible that recruitment may be a recurrent problem in fragmented populations of species such as *F. b. feldeggii.* Although no long-term studies exist, many breeding sites become empty when one of the partners disappears and several nesting sites on cliffs were occupied by single adults (Leonardi *et al.* unpubl. data).

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FIGURE S43 A perching sub-adult *F. b. biarmicus* in the Mata Mata area of the Kgalagadi Transfrontier Park in South Africa. © and courtesy of Monique E. Adams.

Chapter 6.
Breeding strategies

6.1 Nesting locations

The Lanner falcon typically breeds on rocks and cliffs but alternative nesting sites are often used across several parts of the species distribution (Table 6.1). Generally, *F. b. feldeggii* seems to be most strictly associated with rocky cliffs while *F. b. biarmicus* is the race most likely to exploit different nest locations. In southern Africa, a total of 72% of Lanner falcon nests were on cliffs, quarries, and buildings while only 28% were in disused nests in trees, on pylons, or on telephone poles (Stephenson 2001). Similarly, in a comprehensive survey of nest sites in the former Transvaal (n = 175), preferred locations were on cliffs (57%), but with the majority found on small cliffs (45%) less than sixty metres in height. Other locations were in disused crows nests on pylons (25%), on crow or eagle nests in trees (14%), and on buildings or in quarries (4%) (Tarboton and Allan 1984). In the same area, Steyn (1983) reported that 68% of nesting sites were on cliffs (n = 91). Thus, the use of alternative

FIGURE 6.1 Lanner falcon perched on a World War II era convoy marker in central-northern Sudan. The ground nest with eggs was on the base covered by fuel tins © and courtesy of C. Vance Haynes.

nesting sites by the Lanner falcon seems to be directly linked with the local presence of nest-building species such as Corvids and other large raptors, as well as the relative abundance of suitable rocky cliffs. In fact, in a sample area of the Eastern Cape Province, only 12% of Lanner falcon pairs used other nest sites which is considerably less than the 37% and 45% observed in other regions of South Africa (Jenkins 1995, Stephenson 2001). Similarly, in the Pretoria area, Lanner falcons typically breed mainly on pylons with only a few pairs usually found on rocky cliffs, both on natural ledges and on old Black Eagle nests (Kemp 1993).

6.2 Rocky cliffs

Main features

Several geomorphological and habitat features seem to be linked with occupancy of rocky cliffs by the Lanner falcon (see also 4.3; Amato *et al.* 2014). In Morocco, *F. b. erlangeri* prefers small cliffs bordering valleys created by intermittent or ephemeral surface water (oued/wādī) or in hilly areas (Jebel/Jbel/Djebel) (Barreau and Bergier 2001). Eight nesting cliffs monitored between 1997 and 2000 in the Eastern Cape region of South Africa were situated in river gorges (Stephenson 2001). In Gambia, *F. b. abyssinicus* mainly used '*kopjes*' (isolated hills in flat, open plains or inselbergs as in the desert areas of Mali or South Sudan) and cliffs (Lynes 1925, Gore 1981). In the Miombo woodlands of Zimbabwe, *F. b. biarmicus* also nests on granite inselbergs within *Brachystegia* woodland. In Zambia, the species usually nests on cliffs and on

Subspecies	Cliffs	Trees	Man-made structure (Pylons, buildings)	Ground
F. b. feldeggii	●●●	●	●	
F. b. erlangeri	●●●	●●	●	●
F. b. tanypterus	●●●	●	●	●
F. b. abyssinicus	●●●	●●	●	
F. b. biarmicus	●●●	●	●●	

Table 6.1 Relative frequency (1-3) of nest type choice by the Lanner falcon races (Warthausen 1860, Cochrane 1864, Irby 1895, Erlanger 1898, Sharpe 1904, Butler 1905, Hartert 1915, Raw *et al.* 1921, Lynes 1925, Coltart 1952, Stanford 1954, Mebs 1959, Jany 1960, Kumerloeve 1968, Kellow-Webb and Dingley 1972, Kemp 1972, Newby 1979, Newman 1979, Jennings 1980, Vernon 1980, Irwin 1981, Bergier 1987, Yosef 1988, Ciaccio *et al.* 1989, McGowan and Massa 1990, Goodman and Haynes 1992, Kemp 1993, Ash and Miskell 1998, Azafzaf 1999, Barreau and Bergier 2001, Gilmour 2003, Salewski and Martignoli 2005, Dowsett-Lemaire 2006; Grubac and Velevski 2010, Pavia *et al.* 2012, Bergier *et al.* 2013, Fernandez-Garcia *et al.* 2013 Dowsett-Lemaire and Dowsett 2014).

quite small rocky hills (Dowsett 2009). In central Mozambique, breeding pairs use ledges of small rocky outcrops and also old nests abandoned by other bird species (Parker 1999). In South Africa, *F. b. biarmicus* usually uses small cliffs when these are available but many territories have also been established in areas where electric pylons are used for nesting (Kemp 1993). The same is true for the Lanner falcon in East Africa where the preferred breeding sites are located mainly on cliffs and only occasionally in trees (Britton 1980). In Togo, the species occupies sites on savannah grasslands (Cheke and Walsh 1996).

Nest eyrie

For Mebs (1959), the size of eyries, and so the degree of shelter they offer, is the crucial factor in nest choice, and exerts a greater influence than the relative position of the site on the cliff-face. For example, a nest in Sicily was an oval-shaped cavity (80 cm wide, 60 cm deep and 30 cm high), and the front edge had been modified by arranging rocks and plant tufts so that they formed a natural rampart (Mebs 1959). Another nest site consisted of a small recess (40 × 40 cm) at the base which served as an eyrie and gave the young falcons a degree of protection, but very little freedom of movement (Mebs 1959). The last nest inspected was 5 metres deep and 2 metres high (Mebs 1959).

Generally in regions of Africa such as Ethiopia, Eritrea, and South Africa, the Lanner falcon uses scrapes on cliff ledge and holes in small cliffs that are re-used each year (Craib 1977, Brown *et al.* 1982, Salvo 1984, Ash and Atkins 2009). In the Eastern Cape province, 91% were located under an overhang or in a crevice and were well sheltered from rain (Stephenson 2001). Tarboton and Allan (1984) reported that 64% of cliff-based nesting sites were on bare ledges (88%; $n = 96$) but only provide scattered data regarding the locations of other nests. In Zimbabwe, a nest on an inselberg was a pothole (75 cm long by 31 cm high) (Gilmour 2003). A nest in Tuscany consisted of a hole of 1.5 m^2 (Pezzo *et al.* 1994).

Coastal cliffs

Generally speaking, Lanner falcons do not breed on coastal cliffs but one case was reported in central-southern Sicily in 1983 (*F. b. feldeggii*) which fledged two young (Salvo 1984). Breeding pairs of *F. b. abyssinicus* have also been observed on sea cliffs in Zula Bay in Eritrea (Smith 1957). In Algeria *F. b. erlangeri* usually avoids using sea cliffs as nest sites, but there have been many observations of birds using sites less than a kilometre from the sea (Ledant *et al.* 1981). The same subspecies also breeds on rock cliffs close to the sea in the eastern coastal zone of Morocco, but with much lower frequency than elsewhere in the country (Bergier 1987).

Re-use of nests

Sometimes the Lanner falcon re-uses nests that have already been built on a cliff and subsequently abandoned by another species, particularly Corvids and other species of large raptor (Table 6.2). Figure s45 shows a female *F. b. feldeggii* feeding three chicks in a re-used Golden Eagle *Aquila chrysaëtos* nest in the Marches area of Northern Italy. In Macedonia, *F. b. feldeggii* use of old nests on cliffs made mainly by Raven *Corvus corax*, but also by Egyptian Vulture and Long-legged Buzzard *Buteo rufinus* (Grubač and Velevski 2010).

In Morocco, *F. b. erlangeri* re-used nests in cliffs and trees which had been made by the local species of Raven, *Corvus corax* in northern regions and *Corvus ruficollis* in southern regions (Bergier 1987). This practice is especially prevalent in Haouz Province, where 80% of cliff-based nest sites selected by Lanner falcons are former Raven nests (Barreau and Bergier 2001).

The same is true in parts of South Africa, where 37% of nests used by the Lanner falcon in Soutspanberg were abandoned nests of other bird species, and 45% of breeding attempts in the Eastern Cape were in former nests of White-necked Raven *C. albicollis* (Jenkins 1995, Stephenson 2001). Other nests in Eastern Cape Province which were re-used by Lanner falcons had previously been occupied by Black eagle (5%), Black Stork (4%) and Jackal Buzzard *Buteo rufofuscus* (3%), but unusually no re-use of Raven nests was reported from this area (Stephenson 2001). In the southern part of the former Transvaal, old Black Eagle nests are frequently used by two pairs of Lanner falcon, although not necessarily the same eagle nest each year (Craib 1977).

Cliff morphology

Although several studies have described the various rock types which constitute the breeding cliffs used by the Lanner falcon, it seems that the species has no particular preferences with regard to the underlying rock substrate. In fact, altitude, slope, and eyrie characteristics are the main factors influencing nest choice and breeding performance for the Lanner falcon.

It seems that a wide range of rock types can be used for nesting sites, including sandstone, gypsum, and calcareous rock which are the main substrates of cliffs selected by *F. b. feldeggii*. However, birds can also be found on cliffs composed of magmatic, limestone, conglomerate, and granite (Mirabelli 1982, Salvo 1984, Ciaccio *et al.* 1989, Siracusa *et al.* 1991, Battista *et al.* 1995, Grubac and Velevski 2010, Mancuso and Gatto 2014).

In Zimbabwe, the selection of sites for breeding is highly variable ranging from large cliffs to the most insignificant pile of boulders (Thomson 1984). Generally,

	F. b. feldeggii	*F. b. erlangeri*	*F. b. tanypterus*	*F. b. abyssinicus*	*F. b. biarmicus*
Corvus corax	●●	●●			
Corvus albus				●	●
Corvus albicollis					●●
Corvus ruficollis		●●			
Neophron percnopterus	●				
Buteo rufinus	●				
Milvus migrans			●		
Circaetus cinereus					●
Aquila fasciata	●				
Aquila chrysaetos	●				
Aquila verreauxii					●●

Table 6.2 Nesting sites of various raptor and non-raptor species re-used by the races of Lanner falcon. ●● = frequent, ● = less frequent (Warthausen 1860, Erlanger 1898, Hartert 1915, Kemp 1972, Craib 1977, Newman 1979, Vernon 1980, Irwin 1981, Brown *et al.* 1982, Mirabelli 1982, Steyn 1983, Bergier 1987, Ciaccio *et al.* 1989, Barreau and Bergier 2001,Barry 2004a,b, Caldarella *et al.* 2005, Grubac and Velevski 2010, Pavia *et al.* 2012).

the sites are isolated but they can also be found along river gorges such as in parts of South Africa or in Inner Anatolia in Turkey (Stephenson 2001, Kirwan *et al.* 2008). In the Cape region, Sharpe (1904) reported a nest in a high *kopje* while a nest-site in Inner Anatolia was on a 100-metre high cliff (Kirwan *et al.* 2008).

In central-southern Sicily, small cliffs up to 30 metres high are typically used by the Lanner falcon, with the nest usually located on the upper parts (Salvo 1984). In Sicily, 90% of breeding cliffs are < 50 m height (range 10–150 m, average 35 m, n = 19) (Ciaccio *et al.* 1989; Figure 6.2). A similar trend is apparent in Campania, where the height of the nesting cliff ranged from around twenty to thirty metres (Mancuso and Gatto 2014). A nest of *F. b. erlangeri* has also been found in a cleft on quite low rocky cliffs in Tunisia (Whitaker 1905). In Sceleidima in Libya, the nest ledge was located two metres above ground level and consisted merely of a hollow scooped in the sandstone. Another nest in the same area was in a deep pot-hole, around 18 metres down (Stanford 1954).

At Djebel Sidi Ali Ben Aoun in Tunisia, the nest was only 5–8 metres above ground level (Erlanger 1898). Similarly, a nest site of *F. b. feldeggii* in Tuscany was located ten metres from the base of the cliff and three metres from the top (Pezzo *et al.* 1994). An in-depth analysis of *F. b. biarmicus* nest sites revealed a nest height that ranged from 20 to 220 metres (average 56 m; n = 35) and between 5 and 20 metres for tree sites (MacLean 1984). Similarly, in Calabria in Southern Italy, nest locations ranged in height from 20 to 250 metres, which is higher than sites in Apulia (10–115 m) and Sicily (6–100 m; average 20 m) (Mirabelli 1982, Ciaccio *et al.* 1989, Ta-

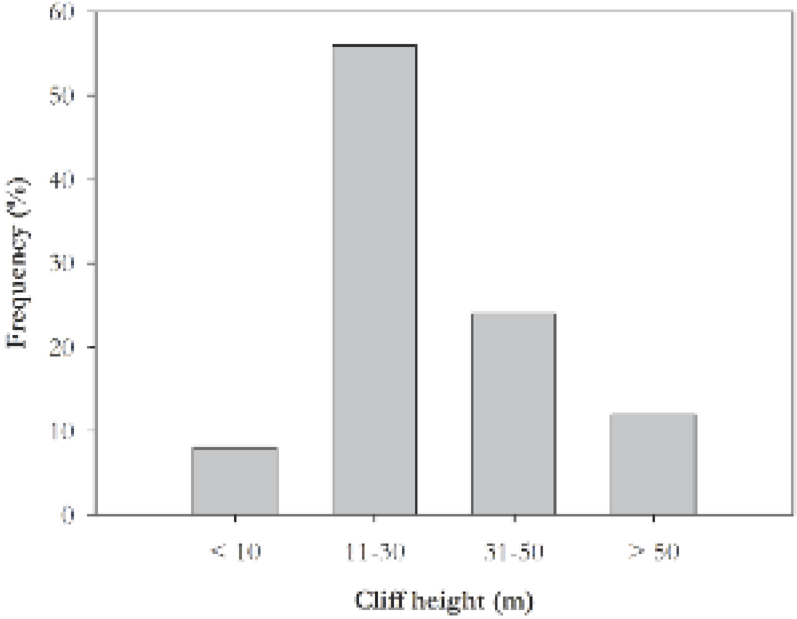


Figure 6.2 Frequencies by height class of preferred breeding cliffs of *F. b. feldeggii* in Sicily (Siracusa *et al.* 1991).

lamo 1998, Caldarella *et al.* 2005).

Several papers have analysed nest locations of the Lanner falcon by dividing the rock face into three regions: upper, medium and lower. For the most part, breeding pairs predominantly tend to use the upper or median third (Mebs 1959, Ciaccio *et al.* 1989, Gilmour 2003, Laterza and Cillo 2008). Despite this trend, it is also apparent that choice of nest site by the Lanner falcon is mediated by the presence of suitable eyries (such as ledges or holes) and the relative abundance of vertical portions of cliff face. Thus, as Stephenson (2001) states, from a hundred-metre high cliff the mean vertical should be only 50 metres. Considering that safety from terrestrial predators would also be a factor in the selection of nesting site, it would be expected that higher cliffs would be chosen more often in preference to lower sites. In fact, there are some cases of nests being located less than five metres above ground level, despite the seeming availability of other eyries nearby at greater heights (Leonardi *et al.* unpubl. data, Ciaccio *et al.* 1989).

Cliff orientation

Figure 6.3 summarizes the available data with regard to aspects of cliff sites where Lanner falcons are known to breed. This comprehensive analysis show a clear pre-

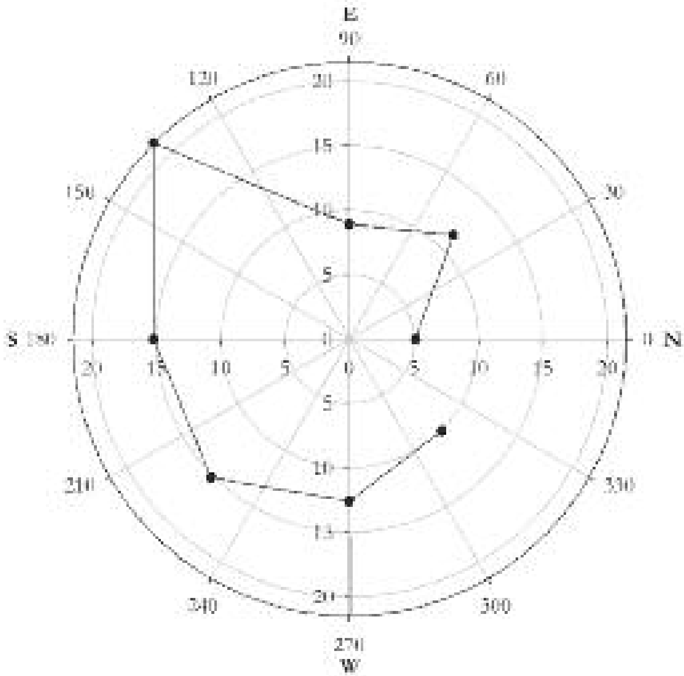


FIGURE 6.3 Cliff aspects (n = 88) of sites where the Lanner falcon races breed (Mebs 1959, Salvo 1984, Mascara 1986, Yosef 1988, Bassi *et al.* 1992, Pellegrini *et al.* 1993, Battista *et al.* 1995, Talamo 1998, Stephenson 2001, Fanfani *et al.* 2002, Gilmour 2003, Caldarella *et al.* 2005, Laterza and Cillo 2008).

ference towards orientation to the south and south-east (Figure 6.3). Cliff sites in the former Transvaal region of South Africa with a west, south-west, or north-west facing aspect were significantly less frequently used than sites facing other directions (n = 46; Tarboton and Allan 1984). Although sites with a north-facing aspect seem to be avoided, in the arid areas of Israel two known nest sites are located on cliffs that face north, and these have the advantage that they are shaded during most hours of the day (Yosef 1988). Based on quantitative data in a study from the Eastern Cape Province, Stephenson (2001) shows that there is a clear link between the number of chicks fledged per nesting site and cliff orientation (n = 22, p = 0.008). On the other hand, a recent study conducted in eastern Sicily failed to find any correlation between shade on nest position and mean productivity (Amato *et al.* 2014).

6.3 Trees

Usually the Lanner falcon chooses to breed on a rocky cliffs but when suitable sites are not available the species will re-use abandoned tree nests of other bird of prey (Table 6.2; Newman 1979). It is also capable of using, for example, Eucalyptus plantations where no cliffs are available, and also breeds in urban areas in a number of towns (Brown *et al.* 1982). Nevertheless, *F. b. feldeggii* in Italy breeds exclusively on cliffs and the sole successful breeding attempt on a Pine *Pinus pinea* tree at Castelfusano wood dates back to 1911, although two young were produced (Martorelli 1911). They are also several very famous nesting attempts on former Common buzzard *Buteo buteo* and *Milvus* sp. nests on Pine trees in Coto del Rey, Coto Doñana, and Corio del Rio by *F. b. erlangeri* (Warthausen 1860, Coltart 1952, Lord Lilford quoted in Coltart 1952, McGowan and Massa 1990). In Arada in Chad, a chick (*F. b. abyssinicus?*) was found in a nest built on a leafy specimen of *Maerua crassifolia* (Newby 1979).

In Zambia, the Lanner falcon breeds as often in abandoned raptor nests in trees as it does on cliffs (Benson *et al.* 1971, Dowsett *et al.* 2008). In Ethiopia and Eritrea the species also frequently uses disused large nests of other species in trees (Ash and Atkins 2009). In the Maghreb area of the Western Sahara, the birds used Acacia and Pistacia trees and *Tamarix* sp. bushes (Jany 1960, Heim de Balsac and Mayaud 1962). In a desert area of Mauritania, a *F. b. erlangeri* brood was found in an isolated stand of about twenty *Acacia tortilis* trees (Salewski and Martignoli 2005). In Zimbabwe, a *F. b. biarmicus* pair used an old stick nest of Bateleur *Terathopius ecaudatus* on Wild Teak *Pterocarpus angolensis* (*Fabaceae* family; Barbour 1971). The Wild Teak was bare of leaves in October and November, during the breeding season, so the site offered no camouflage or shelter from the sun (Barbour 1971). The nest was in a fork, nine metres above ground level, and the Lanner falcon had made no addition to it (Barbour 1971). It seems that the Lanner falcon re-uses Bateleur nests quite often and in fact there are at least four recorded cases, with Barbour (1971) adding another one (Steyn 1983).

In Kodok in South Sudan, an old nest used by *F. b. abyssinicus* was located six metres up in a *Balanites aegyptiaca* (*Zygophyllaceae* family) tree (Lynes 1925). In Accra in Ghana, *F. b. abyssinicus* also breeds in trees, such as *Antiaris* (*Moraceae* family), taking over the nests of other bird species (Dowsett-Lemaire and Dowsett 2014). In Zimbabwe, *F. b. biarmicus* reused old Hamerkop *Scopus umbretta* nests which were located in the forks between trees branches (Thomson 1984). In eastern Zambia, the Lanner falcon breeds in disused nests in various woodlands but these are often difficult to locate and the population density in these habitats is probably much lower than in areas with cliffs (Osborne and Colebrook-Robjent 1984).

In Mzab in southern Algeria, former Raven nests on Terebinth trees *Pistacia terebinthus* (*Anacardiaceae* family) are re-used by Lanner falcons, particularly in the small oases between Laghouat and Ghardaia (Hartert 1915). In Kenya, northern Nigeria, and Ethiopia, in areas of tall introduced *Eucalyptus* trees, the nests of Pied crows were preferred to those of Cape Rook (Brown *et al.* 1982). In the Vaal Dam district (on the border between Gauteng and Free State), only a few resident pairs of Lanner falcons were found due to the presence in the large *Eucalyptus* plantations of only one nest type which had been built by African Fish Eagles. In this case, if a nest site was reoccupied or destroyed it meant that there were fewer available nest sites for Lanner falcons (Craib 1977). From the available records, it therefore seems that the use of trees as nesting sites by the Lanner falcon is wholly dependant on the presence of other species that do build nests.

Trees are also regularly used as perch sites by all subspecies of Lanner falcon and Bree (1859) states '*It used to perch on high palms or high trees and also near ruins or human settlements*'. Lanner falcons are also known to perch on dead trees of species such as *Acacia erioloba* along the Nossob river in South Africa.

6.4 Ground-nests

When there are no cliffs, trees, or rock outcrops available the Lanner falcon can nest on the ground, a behaviour which has been observed, for example, in southern Algeria. A nest has also been found on the ground in northern Mauritania in plain sandy desert with no trees nor cliffs in the vicinity (Salewski and Martignoli 2005). The frequency of ground nesting is, however, low and can lead to reduced productivity, as in Morocco for example where egg deposition on bare soil is half of that found in sites in re-used nests (Bergier 1987). In the Western desert along the Egyptian-Sudanese border, nests were located on the ground due to the total absence of terrestrial predators (Figure s19; Goodman and Haynes 1992). Interestingly this site also revealed distraction behaviour in the Lanner falcon. When confronted with human presence at the nest site, the brooding parent started to show '*broken wing*' behaviour, and after crawling for a few metres, finally flew off (Salewski and Martignoli 2005).

6.5 Man-made structures

The first observation of nesting by Lanner falcons on man-made structures was made in Egypt by Cochrane (1864). He visited a nest on the south side of the Third Pyramid which was around nine metres from the top and which contained four eggs (two addled, two incubated). In 1870, another clutch of five eggs was collected at the Third Pyramid (Cavendish Taylor 1878). Thus, Shelley (1871) considered the Lanner falcon a regular breeder at the Pyramids. Nevertheless, Raw *et al.* (1922) did not find any traces of breeding pairs in the pyramids of Gizeh. Warthausen (1860) wrote that the Lanner falcon had not nested in the Pyramid of Cheops in May 1851 as had been previously reported by T. von Heuglin. Several previous Authors reported local people collecting eggs and live birds (including adults), or shooting them, for the benefit of tourists. As evidence of this, Cochrane (1864) reported the

Figure s44 An adult Lanner *F. b. erlangeri* perched on an electricity pylon in Morocco. © and courtesy of Peter Jones.

Figure s45 Female *F. b. feldeggii* feeding three chicks in a re-used Golden Eagle nest (Marches, Italy). © and courtesy of Bruno D'Amicis.

capture of a brooding female inside her nest during the night. In central-southern Sicily, nests have been located in an ancient necropolis made on the rocky cliffs by the ancient population known as the Sicanians (Salvo 1984). In Tunisia, the Roman aqueduct at Mohammedia is regularly used as breeding site by *F. b. erlangeri* (Azafzaf 1999). Other famous nesting sites on ancient man-made structures are at the Meroë pyramids in Sudan, on the north side of the second pyramid of Gizeh, and at Dahshur in Egypt (Cochrane 1864, Warthausen 1860, Butler 1905).

In Africa, power lines provide the main roosting, nesting, and perching sites for territorial Lanner falcons (Figure s36; Kemp 1993). The use of pylons is similar to the use of old nest in trees but occurs with much less frequency where tree-nesting occurs (Kemp 1972). It is possible that fledging success on pylons is less than natural breeding sites (Brown *et al.* 1982) although the increase in the numbers of breeding pairs of Lanner falcon during the 1980s may have been due to the use of old nests in pylons (Brown *et al.* 1982). In fact, fifty percent of the breeding sites in the Highveld areas in the former Transvaal Province of South Africa were on electricity pylons (Tarboton and Allan 1984). In addition, the establishment of a network of new electricity transmission lines in South Africa and Namibia appears to have extended the distributional range of the Lanner falcon through the creation of new breeding sites where there were none previously (Tarboton and Allan 1984, Brown and Lawson 1989). In this case it seems that the nests of Cape Crows *Corvus capensis*, and less frequently of Pied Crow *C. albus*, on twenty-five metre high electricity pylons has aided the spread of Lanner falcons into new formerly unoccupied areas (Brown *et al.* 1982, Kemp 1993). Nevertheless, there are some additional risks associated with the use of these sites. For example, one report describes a *juvenile* female flying downwind that collided with the nest pylon breaking its right wing and severely lacerating its face and body (Kemp 1993). The tendency for other Lanner falcon races to nest on pylons is not clear, although in the second half of April an individual of *F. b. erlangeri* was found in a nest on a pylon in central-eastern Tunisia (H. Azafzaf pers. comm.). In Macedonia, *F. b. feldeggii* used an old nest of Raven *Corvus corax* in a pylon but no other sightings have been made with regard to any other European countries (Grubač and Velevski 2010).

Of four nesting sites recorded in Darb el Arba'in Desert in south-western Egypt, one was on the floor of a World War II truck and another one in an old British army camp (Figure 6.4; Goodman and Haynes 1992). Lanner falcons also used the side mirrors of the lorry and the empty petrol tins as favourite perches (Figure 6.1; Goodman and Haynes 1992). Other man-made structures can be used by the Lanner falcon and it has been recorded nesting at Oribi Airport in Pietermaritzburg, KwaZulu-Natal (Byron and Downs 2002). Lanner falcons have also been observed at the Kimberley 'big hole', an open-pit and underground mine in South Africa (Anderson 2000). In Namaqualand, a Lanner falcon was found using an abandoned nest

Figure 6.4 A female *F. b. tanypterus* in a World War II lorry used as nest site (South western Egypt; © and courtesy of C. Vance Haynes).

of a Cape Rook on a windmill, with the piston of the pump moving up and down through the middle of the nest (Brown *et al.* 1982). In large towns, many Lanner falcon nests are found on buildings, making use of any available site, and even possibly using the small stick nest of a Speckled Pigeon *Columba guinea* as a foundation as has been observed at a site in Addis Ababa, Ethiopia (see also 6.7; Brown *et al.* 1982).

6.6 Breeding in desert areas

'*In the south-west corner of the Egyptian Western Desert and adjacent Sudan, Lanners return to the vast and barren sand sheets in early February and commence breeding*'. Goodman and Haynes (1992) wrote these remarks about the Lanner falcon population (*F. b. tanypterus*) which breeds in the Darb el Arba'in Desert. In 1955 E. Jany remarked that even in the remoteness of the desert areas of Serir Tibesti in Libya and Chad, Lanner falcon pairs breed where no other bird does (Jany 1960). Nevertheless, as R. E. Moreau states, the Lanner falcon is not a true desert bird, and is more often found in the neighbourhood of oases, although birds have been found on fragmentary outcrops of rock in full desert. Its presence in the desert is dependant on the spring migration of prey species and it departs shortly after breeding. Unlike the Sooty falcon *F. concolor*, the Lanner is not a specialist species that is confined to Saharan habitats but is strictly an opportunist and seasonal resident.

The nest described by Jany (1960) at Serir Tibesti was on a rock outcrop bordering Wadi el-Faregh. It was five metres lower than the gravel desert and around two metres from its steep south-facing face (Jany 1960). The nest entrances were from the east and south-west (Jany 1960). Jany (1960) also reported that the nest exposure permitted sunlight to hit the nest in the morning and late afternoon which may have proved useful against low air and soil temperatures (which were 10°C at 5:00 am and 7°C at 6:00 pm respectively). Nevertheless, some of these presumed effects of thermal insulation that could be predicted from the cliff orientation in desert zones such as in parts of Morocco seem to have no influence on choice of nesting sites (Bergier 1987).

The extreme environmental conditions and scarce food supplies associated with desert areas clearly have a great deal of influence on both breeding biology and productivity. Isenmann and Moali (2000) suggest that pairs breeding in the desert areas of southern Algeria lay at least two eggs in March whereas in the north at Great Kabylia the range is 3–4 (Feb–Mar; see also *Eggs*). Among two nests close together, Jany (1960) observed a lapse of around fifteen days with one nest containing unhatched eggs and the other with chicks. Such a gap could be crucial for the success of the breeding season due to the synchronization of breeding with the spring passage of prey. The importance of this timing was confirmed by the remains of dead chicks of past season at the same nest (Jany 1960).

A preliminary survey on diet by means of pellets analysis (n = 14) confirmed a complete predominance of trans-Saharan avian prey, as well as at least one *Gerbillus* sp. (Jany 1960). Migrating birds are very easy to capture in this harsh environment due their low-level flight, and prey species include *Upupa epops*, *Motacilla flava*, *Coturnix coturnix*, and *Streptopelia turtur*. These are all species migrating from their sub-Saharan wintering grounds to Eurasian breeding areas (Jany 1960, Goodman and Haynes 1992). The diet of Lanner falcons in the eastern desert is almost totally made up of avian prey, although the remains of locusts *Schistocerca gregaria* were also relatively common (Goodman and Haynes 1992). A certain degree of mortality at the chick stage most probably occurs in these extreme environments as confirmed by the mummified remains of Lanner falcon nestlings found near nests (Jany 1960, Goodman and Haynes 1992). Bergier (1987) also reported a high rate of mortality (around 75%) of young birds in the desert areas of the High Plateau of Morocco. In areas of the central Sahara at Jikara in Niger, the Lanner falcon breeds on isolated outcrop surrounded by sandy desert areas and birds have been observed on nests in March (Newby 1981). The species has also been recorded breeding on isolated granite outcrops in Arabia, in a desert area south-west of Riyadh and it was present in both the Eastern Province at Abqaiq and Central Province at Thumamah in the 1980s (Jennings 1980). In the Western Sahara region of Morocco, an *F. b. erlangeri* nest with three young of 2–3 weeks old was found in early April (Bergier *et al.* 2013) and similar observations of nests in April have been made at Kufra Oasis in Libya. In nests located in the Negev desert, egg laying took place in late February, the eggs hatched in the third week of March, and young fledged at the end of April (Yosef

1988). In southern Algeria, ground nesting has been reported, as well as re-use of old nests of *Corvus* sp. In the northern desert of Mauritania during the first week of April, one-week-old chicks and an unhatched egg were found in a ground nest, and at around the same time a tree nest in an Acacia tree contained young birds (Salewski and Martignoli 2005). Where possible, the Lanner falcon will make use of isolated trees, either dead or alive, such as in Chad where species such as *Maerua crassifolia* are used, or in the Western desert where Acacia species are often favoured (Newby 1979, Bergier *et al.* 2013).

Given the importance of the passage of migrant birds as a source of prey to feed chicks, and that these migrations occur along a precise route, it is possible to predict a non-random distribution of breeding pairs that should result in a higher density of pairs nesting close together under migration routes. In February 1933, seven pairs of Lanner falcons were found to be occupying two rock outcrops located 110 and 190 kilometres south and west of the Farafra oases. In the Judean Desert and the northern and central Negev mountains, Frumkin (1986) reported nine territorial pairs, three nests, and sixteen more sites where the presence of Lanner falcons had been recorded. More accurate surveys in these Israeli deserts revealed an underestimation of the breeding populations of Lanner falcons in the region. In fact, the population increased from 2 bps (7–9 individuals) in 1980 to 3–7 bps (18–34 individuals) in 1984 (Frumkin 1986).

6.7 Urban Lanner falcons

The Lanner falcon regularly breeds in several large towns in Africa, including Addis Ababa, Nairobi, Durban, Harare, and Pretoria (Table 6.3; Sinclair and Walters 1976, Getraide and Hatzofe 1990, Brown *et al.* 1982) and it is also present in small towns or villages throughout the continent, such as in Ghana where it is present in Accra and Nakpanduri (Dowsett-Lemaire and Dowsett 2014). The numbers of breeding pairs located in urban areas could therefore not be insignificant. For example, there are at least three pairs breeding in the central business district of Harare in Zimbabwe, and this number is probably an underestimate given the existence of large numbers of crow nests (Deacon *et al.* 2002).

Lanner falcons can often be seen flying over towns in Ethiopia and Eritrea, and can be observed sitting on lamp-posts in the centre of Addis Ababa (Guichard 1950, Ash and Atkins 2009) and have even been recorded at sea off Accra, with the bird coming on board a ship (Dowsett-Lemaire and Dowsett 2014). An adult was found stunned after striking a window in Harare and a female after striking a window in Chitungwiza (Mundy and Hartley 2002), and Lanner falcons have been observed hunting pigeons in the central district of Johannesburg in South Africa. In Uganda, on the other hand, the species seems to be distinctly scarce in urban areas including

Location	Productivity
Harare, Zimbabwe (1970s)	3.2 (n = 2)
Pretoria, South Africa	2.5 (n = 1)
Harare, Zimbabwe	3.4 (n = 5)

Table 6.3 Mean productivity of pairs of urban Lanner falcons in large towns in southern Africa (Kellow-Webb and Dingley 1972, Kemp 1993, Deacon *et al.* 2002).

around Kampala (Carswell *et al.* 2005).

The Lanner falcon has also been observed in urban areas in many other countries. Large groups have been seen over Sana'a, five being seen together in September for example, and it is regularly sighted over Taiz in North Yemen (Phillips 1982). At Lahej, also in Yemen, they may be found resting in shade during the heat of the day on the Sultan's palace and also in palm trees. In the Palearctic, *F. b. feldeggii* does not seem to be present in large towns, although it is sometimes found in villages close to nest sites in Sicily and Tuscany. In Apulia, it is very rare to observe Lanner falcons over towns and villages although they have been seen at Foggia, Monte S. Angelo, and Manfredonia, where a low-flying male was observed hunting over a wheat small field in the outskirts (Caldarella *et al.* 2005).

In large towns, the Lanner falcon has been found nesting on buildings most often in small urban areas surrounded by large portions of natural environments (Deacon *et al.* 2002). A breeding pair in Harare (Zimbabwe) used a flat narrow concrete ledge (10 m × 1 m) on the twelfth floor separated from the interior by a low wall (Deacon *et al.* 2002). The nest entrance was 1.5 metres and overlooked a small wooded square but they also used a nest box placed in the corner of the ledge which was installed when the female first laid an egg on the bare cement of the ledge (Deacon *et al.* 2002). In Addis Ababa in Ethiopia, birds make use of small disused nests of Speckled Pigeon *Columba guinea* as a foundation (Brown *et al.* 1982). The site chosen in Durban was a draining ledge 105 m from the ground, giving the birds a clear view of the city (Sinclair and Walters 1976).

As has been observed in natural environments, pre-fledging mortality at urban sites is low (Table 5.3). In Harare for example, pairs fledged seventeen out of nineteen young (89.5%) and only one chick perished on the ledge before fledging (Deacon *et al.* 2002). Many of the fatalities after fledging were due to prematurely fledged young that fell down on to the road below (18% of fledged birds) where they were unable to find any refuge (Deacon *et al.* 2002) and two attempts by a young female and a young male to return to the nest were unsuccessful (Deacon *et al.* 2002). Kemp (1993) also recorded a high rate of mortality among chicks raised in Pretoria. In addition, a high rate of unhatched eggs occurred during his four-year study period, with three clutches failing out of a total five (Kemp 2003). Although both parents are usually tolerant of humans, sometimes aggressive behaviour such as open wing displays and hissing can occur (Kellow-Webb and Dingley 1972). One of the female parents of a pair nesting in Harare became very habituated to human presence, and often perched close to a window observing activities inside the building. Nevertheless, despite this continued contact with humans she vigorously defended her brood from a photographer inside the office (Deacon *et al.* 2002). Supplementary feeding in the form of whole mice was offered and accepted by the female, who distributed them to her brood (Kellow-Webb and Dingley 1972) Cities are not particularly rich in terms of food resources and it is possible that Lanner falcons resort to searching for prey such as *Streptopelia* doves outside the city centre (Deacon *et al.* 2002). In central Harare in Zimbabwe, prey brought to the nest by parents included doves, small mammals, passerines, and on two occasions a budgie and a bat (Kellow-Webb and Dingley 1972). A more detailed study of the diet of urban Lanner falcons in the same town shows a strong prey predominance of prey from two avian groups (Doves and Swifts) and very low percentages of other birds, mammals, and arthropods (Figure 6.5). In Durban (South Africa), the main feeding area for the breeding pairs appeared to have been the bayhead, where thousands of Columbiforms (Laughing and Red-eyed Doves and Feral Pigeons) feeding on the dump and waders

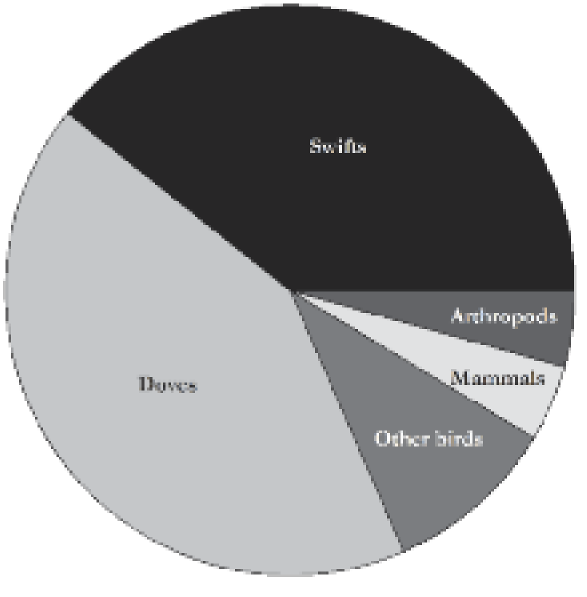


FIGURE 6.5 Frequencies of prey provided to young by Lanner falcon parents in urban areas (Deacon *et al.* 2002; Swifts = *Cypsiurus parvus*, *Apus affinis*, *Apus* sp.; Doves = *Streptopelia capicola*, *S. Senegalensis*, *S. Semitorquata*; Other birds = *Vanellus coronatus*, unidentified small birds; Mammals = *Rattus rattus*, Arthropods = *Acrididae* sp.).

Subspecies	Urban area	Status
F. b. erlangeri	Timimoun, Algeria	Obs
F. b. tanypterus	Cairo, Egypt	Br
F. b. abyssinicus	Ougadougou, Burkina Faso	Br
F. b. abyssinicus	Addis Ababa, Ethiopia	Br
F. b. abyssinicus	Toumodi, Lamto, Ivory Coast	Br
F. b. biarmicus	Harare, Bulawayo, and Chitungwiza, Zimbabwe	Br
F. b. biarmicus	Kampala, Uganda	Br?
F. b. biarmicus	Pretoria, South Africa	Br
F. b. biarmicus	Johannesburg, South Africa	Br
F. b. biarmicus	Durban, South Africa	Br

Table 6.4 Large and small town where the Lanner falcon has been recorded. Obs = *observations*, Br = *breeding* (Raw *et al.* 1921, Kellow-Webb and Dingley 1972, Sinclair and Walters 1976, Irwin 1981, Ledant *et al.* 1981, Brown *et al.* 1982, Leonardi *et al.* 1992, Kemp 1993, Mundy and Hartley 2002, Carswell *et al.* 2005).

(Ruff and Grey Plover) using the estuary (Sinclair and Walters 1976).

6.8 Occupancy

A long-term study of Merlins *F. columbarius* provided evidence that bird quality, and to a lesser extent nest-site quality, influences reproduction in a natural population (Espie *et al.* 2004). The site-dependent population regulation hypothesis (Espie *et al.* 2004) predicts that the quality of nesting sites may have a large influence on breeding performance, especially in raptor species which show a strong territorial fidelity. As is to be expected based on this theory, the mean number of young fledged *per* territorial pair of Lanner falcons in eastern Sicily was positively related to occupancy rates (Figure 6.6; Amato *et al.* 2014). In fact, a very few high quality nest-sites raised 58% of the total young produced across the whole study area (Amato *et al.* 2014). This local trend with regard to occupancy rates is confirmed by scattered data published as a result of studies from other areas (Figure 6.7).

Thus, high-quality nesting sites should tend to be re-occupied every year, and also remain occupied over long periods of time. For example, a nesting site in Sicily which was recorded as occupied in 1936, was subsequently recorded as being occupied in 1957 and also during the 1990s and 2000s (Orlando 1957, Mebs 1959). A nest site at the Roman aqueduct in Tunisia was re-occupied each year by pairs of *F. b. erlangeri* (Figure 3.1; Azafzaf 1999). A recent study made on a breeding population of Lanner falcons revealed a significant relationship between productivity and vocal activities, which may be an indirect measure of quality in male partners (Leonardi *et*

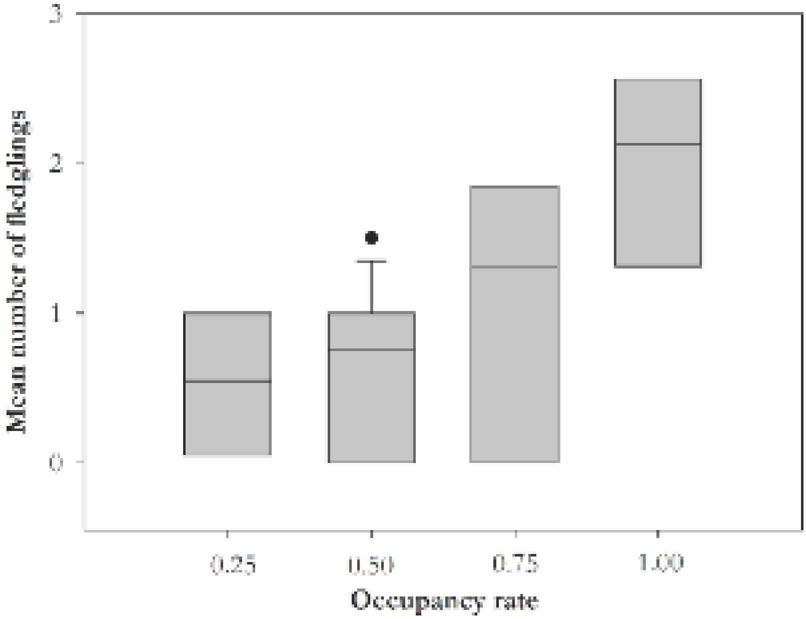


FIGURE 6.6 The relationship between mean number of fledglings per territorial pair of Lanner falcon and occupancy rate of nest-sites in eastern Sicily (Amato *et al.* 2014).

al. 2013). Thus, both internal and external factors are likely to act in combination to constrain breeding performance (Espie *et al.* 2004).

Although Lanner falcons frequently changed nest eyrie on the same cliff, it is also the case that the same nest site may be used year after year, especially cliff sites, and in some cases sites that have not had resident birds for a number of years will be re-occupied (Stephenson 2001), although some sites may also only be used once during a specific study period (Stephenson 2001). It seems that low-quality sites are used only infrequently over a period of time and could well represent alternatives to more preferred high-quality ones (Amato *et al.* 2014). Unfortunately, it is therefore possible to overestimate the number of actual nesting pairs due to the presence of sites with low occupancy rates (Amato *et al.* 2014). For example, a pair changing nest-site over the course of several years may be counted several times in subsequent breeding seasons leading to an overestimate of the population (Amato *et al.* 2014).

In Kleinfontein (Gauteng, South Africa), breeding pairs used different pylons each year for a six-year period (Kemp 1993). In Rietvlei (KwaZulu-Natal, South Africa), a pylon was used for five years then another one 2.8 kilometres away was during the sixth year. The first one was used again for the first clutch, and the second again for a replacement clutch (Kemp 1993). A pair in the town centre of Pretoria repeatedly used the same artificial nest tray for five years (Kemp 1993). In South

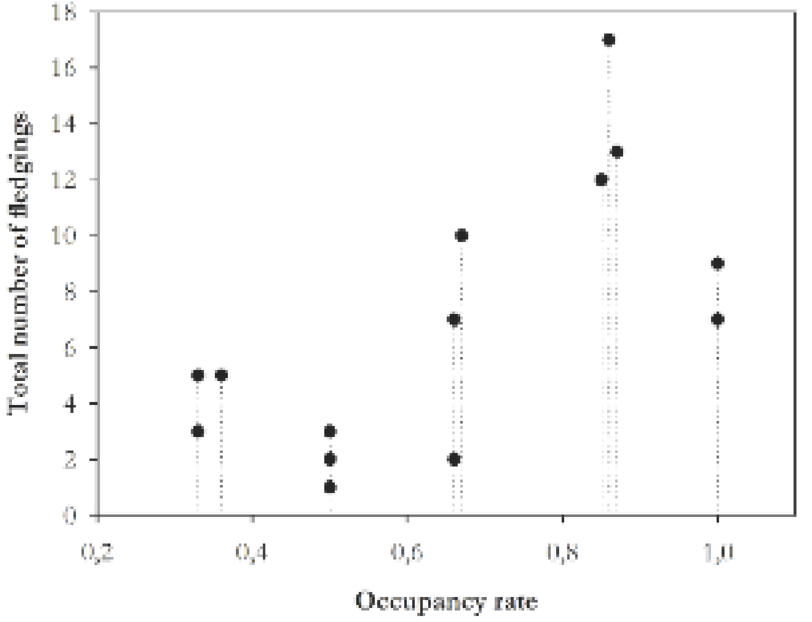


FIGURE 6.7 Occupancy rates and total number of fledglings produced per site in different parts of the distributional area (Chaivetta 1982, Salvo 1984, Kemp 1993, Talamo 1998).

Transvaal, a group of five nests has been regularly monitored, three of which have been used for at least the last four years (Craib 1977).

Sites with high occupancy rates have a key role to play in population trends because they contribute a disproportionately large number of fledglings, but it is also fundamental to evaluate the effective contribution of low-quality sites for the overall persistence of a viable population (Amato *et al.* 2014).

Chapter 7.
Diet and hunting techniques

7.1 Prey

Given that it is a species that is very widely distributed, it might be expected that the Lanner falcon exploits a wide range of possible prey and that the composition of its diet is correspondingly diverse. However, in common with other large falcons and particularly with other species of Hierofalcons, the Lanner falcon is a specialist predator of birds (Leonardi 2001), although mammals, reptiles, and invertebrates are food sources that are often exploited as alternative prey in varying percentages (Leonardi 2001).

In Pretoria, birds formed 79% of the diet of Lanner falcons, with doves and pigeons the most frequent prey species, accounting for 43% of the total (Kemp 1993). The diet of Lanner falcons in Emilia-Romagna consisted of 70% small bird species such as Starlings, Larks, and Sparrows, 20% of larger bird species such as Pigeons, Turtle doves, Jays, Magpies, and Grey partridge, and only 10% small mammals and lizards (Chiavetta 1982). The Lanner falcon is also an occasional predator of Swifts

Figure 7.1 An hunting attempt made by a Lanner falcon (*F. b. biarmicus*) at Kwang water hole of the Kgalagadi Transfrontier Park, South Africa. © and courtesy of Brett E. Ellis.

such as the Little Swift *Apus affinis* in the Northern Province of Zambia (Brooke and Vernon 1961). The choice of prey is very dependent on the relative abundance and therefore availability of a particular species. For instance, the relatively new and increasingly common presence of Woodpigeon *Columba palumbus* in the diet of *F. b. feldeggii* is probably related to the recent increase in numbers of this species in Italy (De Sanctis *et al.* 2009). Lanner falcons have also been known to cache food, in order to avoid any shortages in prey availability (Morimando *et al.* 1997).

One of the peculiar characteristics of the Lanner falcon is its tendency to adopt opportunistic feeding habits, which is a significant difference to the feeding habits of the Peregrine. For example, in the Cape Province of South Africa, Lanner falcons frequented a refuse dump where an abundance of prey in the form of *Rhabdomys* sp. could be found, congregating in groups of at least six birds, but often as many as 20–30 are present (Pitman 1967). They have also been known to follow a tractor being used for ploughing or harvesting and in this way species such as Quail finch, Button Quail, African Quail, and Orange-throated Longclaw were struck and retrieved by Lanner falcons after they had been flushed from undergrowth (Stephenson 2001). On two occasions a male was seen to follow a vehicle along a road and catch a weaver and a quail finch that were flushed by the vehicles (Stephenson 2001). This technique has also been reported in East Africa where Lanner falcons feeding along railway lines and seizing on prey such as *Colius*, quails, and doves which had been disturbed by passing trains (Jackson 1938). *F. b. biarmicus* has been observed on several occasions pursuing pigeons wounded by hunters or farmers that are encouraged to shoot pigeons in order to limit crop damage (Stephenson 2001). This behaviour has been reported from as long ago as the early nineteenth century, when Lanner falcons would reputedly follow herders who were hunting quail by throwing sticks, in the hope of snatching crippled birds (Steyn 1983).

Invertebrate species are also exploited when they available in large quantities. Lanner falcons have been recorded occasionally taking adult locusts in the Rukwa valley of south-western Tanzania (Vesey-FitzGerald 1955). They are also known to feed opportunistically on grasshoppers and flying termites that have been disturbed by grass fires (Stephenson 2001).

Sample composition and pellets

As observed by Mormando *et al.* (1997) a methodological bias can affect the analysis of the diet of the Lanner falcon due to differences in the nature of data gathered from plucked remains, pellets, and direct observations. This in turn can lead to differences in estimations of the three main categories of prey (passerine bird species, non-passerine bird species, and mammals) which were found to be highly significant (see also *Prey size*; Morimando *et al.* 1997). Direct observations at the nest showed

FIGURE S46 Pellets and prey remains at a *F. b. feldeggii* site, including ringed legs of racing pigeons from Malta. © and courtesy of Mirko Amato and Adua Ossino.

FIGURE S47 A female *F. b. feldeggii* bringing prey to its favourite perching site (Sicily, Italy). © and courtesy of Markus Varesvuo.

that species of passerine birds were apparently delivered to the nest more frequently than non-passerine species (Morimando *et al.* 1997). Evidence for the presence of larger avian prey species in the diet of Lanner falcons mainly comes from plucking remains, and evidence for the presence of mammals and invertebrates in the diet was only found in pellets (Morimando *et al.* 1997). In fact, some pellets were composed solely of insect remains, mainly species of *Formicidae* and small Coleopterans (Morimando *et al.* 1997). Reliance on plucking data alone may therefore result in overestimates in the numbers of large and medium-sized birds in the diet, and relying on data from pellets alone tends to over-estimate the amount of small passerines and mammals (see *Prey size*; Morimando *et al.* 1997). In a study from Abruzzi where 258 prey items were identified, 7% came from perch sites, 12% from direct observations, 8% from pellets, and 73% from remains in the nest (De Sanctis *et al.* 2009).

Table 7.1 lists measurements of pellets from some of the regions where Lanner falcons are found. Examples of the form and structure of pellets are illustrated in Figure s46. Pellets have a cylindrical oval shape and are variable in colour depending on which prey species have been consumed (Figure s46; Souttou *et al.* 2005). Pellets from *F. b. erlangeri* in southern Algeria were mainly sandy beige and brick-red in colour, but they can also be grey or yellow (Souttou *et al.* 2005). It is possible to identify between one and nine individual prey items inside each pellet (average 3.1 ± 1.6; Souttou *et al.* 2005). In Sicily, Lanner falcon pellets are significantly larger than those of the Peregrine falcons *F. p. brookei* found there (Siracusa *et al.* 1988).

Prey size

Differences in mean weight prey (MPW) have been derived from various collection

Location	Weight	Length	Breadth
Central-southern Sicily	5.7	max 71	max 25
Sicily	–	39.2 ± 10.4	19.4 ± 8.3
Sicily	–	39.4 ± 9.8	18.7 ± 2.4
Sicily	–	39.6 ± 6.9	20.2 ± 1.5
Sicily	–	40.3 ± 9.9	18.9 ± 3.2
Pretoria, South Africa	1.77 ± 0.71	–	–
Central-southern Algeria	–	42.3 ± 10.4	24.2 ± 4.0
Eastern Desert, Egypt	–	35.1 ± 6.9	16.5 ± 3.7

Table 7.1 Dimensions and weights of Lanner falcon pellets recovered from sites in Sicily and Africa (Weight = g; Length and Breadth = mm; Salvo 1984, Siracusa *et al.* 1988, Ciaccio *et al.* 1989, Goodman and Haynes 1989, Massa *et al.* 1991, Kemp 1993, Souttou *et al.* 2005).

methods adopted in the field (Morimando *et al.* 1997). In Tuscany, the MPW of prey brought to the nest was around 121 g, representative of species such as *Sturnus vulgaris* for example. However, the MPW derived from plucked remains was around 182 g, considerably more than that of prey taken to the nest, and corresponds to prey species such as *Picus viridis* and *Garrulus glandarius* (Morimando *et al.* 1997). The MPW in pellets was around 100 g, which was less than that found in plucking, and represents prey species such as *Turdus merula* (Morimando *et al.* 1997).

The mean prey size of 60 g found in a study in central-southern Sicily therefore seems too low (Salvo 1984). Another study in Sicily gave the MPW as 150 g from avian prey, and 117 g overall (Mascara 1986). Also in Sicily, it was found that the MPW of 121 g is considerably more than that of the Peregrine, which is 93 g (Ciaccio *et al.* 1989). Prey species ranged in size from the smallest, which was Stonechat at 14 g, up to the largest, which was Hooded crow at 500 g (Ciaccio *et al.* 1989).

F. b. biarmicus is likely to eat 1,460 Lark-sized birds or 300 Sandgrouse-sized birds each year (Maclean 1996). Birds used in falconry (such as *F. b. tanypterus*) often have difficulty in catching and handling large prey such as Houbara and Hares (Allen 1980). In the wild, such large prey items found in the diet are presumably obtained through kleptoparasitism or necrophagy (Ciaccio *et al.* 1989, De Sanctis *et al.* 2009).

Prey handling and ingestion

When Lanner falcons consume large prey, the neck is eaten first, then the head, and finally the breast muscles (Figure s47). Internal organs are not consumed. In common with other species that feed on avian prey, the Lanner falcon exhibits an efficient approach to ingesting large prey slowly in order to improve the process of digestion (see also *The digestive tract*; Slagsvolt *et al.* 2010). Smaller prey items are, however, ingested complete (Mirabelli 1982).

Role as superpredator

Mebs (1959) found that in Sicily more than 10% of prey consisted of Lesser Kestrels, Eurasian Kestrel, and Little Owl. It is possible that, as the Lesser Kestrel colony was very close to the Lanner falcon sites, encounter rates were correspondingly increased (Massa *et al.* 1991). Massa *et al.* (1991) also found prey remains of Montagu's Harrier, Red-footed falcon, Barn Owl, and Scops Owl in the diet of Lanner falcons. The presence of so many raptor species at the same nest suggests a possible raptor specialization by a single pair of Lanner falcons during the spring passage. Similarly, in the Eastern Desert, *F. b. tanypterus* has been known to feed on other raptor species including Common buzzard, Eurasian Kestrel, and Short-eared Owl *Asio flammeus* (Goodman and Haynes 1992). Lesser and Eurasian kestrels have also been reported as prey in Calabria, and Barn Owls have been taken as prey by *F. b. biarmicus* in the former Transvaal (Mirabelli 1982, Tarboton and Allan 1984). In Israel, a female *F. b. tanypterus* was seen to stoop on a Hobby *F. vespertinus* and knock feathers off, and a captive Lanner falcon has also been known to kill and eat Hobby (Meinertzhagen 1920). In northern Cameroon, the Lanner falcon has been noted robbing the nest of a Grasshopper Buzzard *Butastur ruipennis*, taking either eggs or nestlings (Buij 2012).

7.2 Diet composition

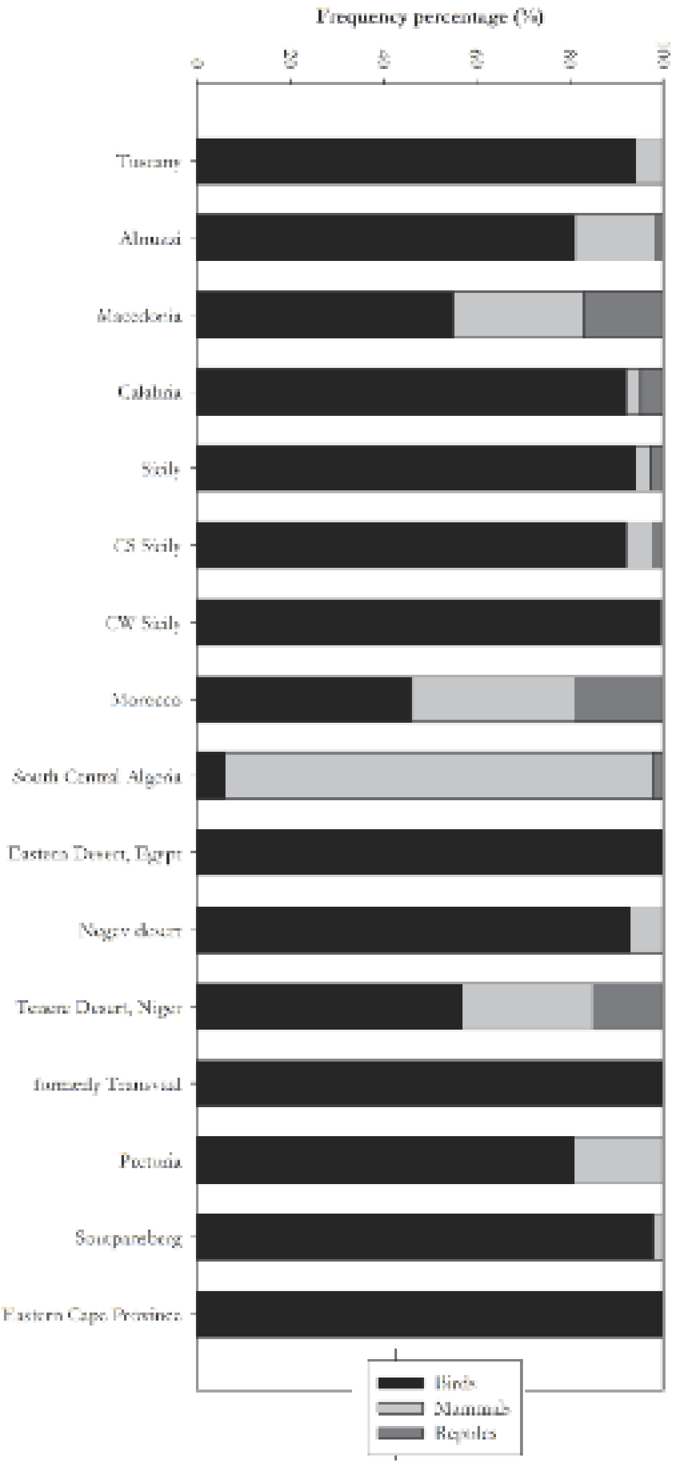
Does the diet composition in different locations reflect the potential use of multiple hunting techniques and the ability of the Lanner falcon to exploit alternative prey? In order to assess this, a basic comparative analysis was made using the available quantitative data and the results are shown in Figures 7.2 and 7.3.

As is evident from the frequencies of the main prey groups in terms of biomass (birds, mammals, and reptiles), in general terms the Lanner falcon is a specialist in avian prey (Figure 7.2). Nevertheless, the exploitation of alternative prey such as mammals and reptiles varies greatly from a minimum of 1% up to an almost total reliance on mammal species, as is the case in the diet of Lanner falcons in central-southern Algeria where there is an almost total reversal of the general trend of avoiding mammalian prey (Figure 7.2). Such marked differences in diet composition are only possible when there is a degree of spatial separation beyond the local level (Figure 7.2). There is no difference, for example, between samples taken from sites in Sicily and Calabria, both of which are in Italy and consequently not subject to a high degree of geographic separation (Figure 7.2).

The ability for a species to switch to alternative prey in response to variability in local environmental conditions or specific food shortages is a characteristic that clearly improves survival probabilities in the face of unpredictable conditions. Does the Lanner falcon show a certain degree of plasticity in its feeding habits in order to overcome such problems? The results of a comparative analysis using Levins' standardized index are shown in Figure 7.3. These results suggest that the Lanner falcon as a species is a relatively specialized predator (B_A = 0.29). In favourable conditions, such as in Sicily and South Africa, a certain increase in the index is seen (B_A = 0.33–0.39). In less favourable areas, such as at the limit of the species distribution in northern Italy, or in harsh semi-desert areas, such as the Negev desert and central-southern Algeria, the value of the index decreases slightly (B_A = 0.24–0.27). Clearly such extreme conditions as are experienced in the Eastern Desert of Egypt are one of the factors that forces the Lanner falcon to specialize on specific prey species during the breeding season (B_A = 0.19).

Diet composition becomes more critical during the breeding period when Lanner

Contents


Frequency percentage (%)
0
20
40
60
80
100
Tuscany
Abruzzi
Macedonia
Calabria
Sicily
CS Sicily
CW Sicily
Morocco
South Central Algeria
Eastern Desert, Egypt
Negev desert
Ténéré Desert, Niger
formerly Transvaal
Pretoria
Soutpansberg
Eastern Cape Province
Birds
Mammals
Reptiles

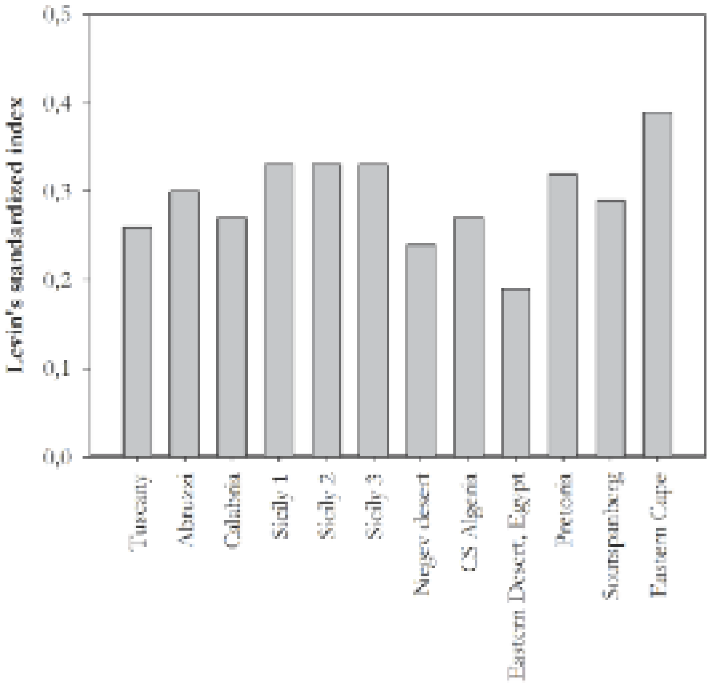


FIGURE 7.3 Comparative analysis of the dietary breadth (B_A) index of the Lanner falcon at various locations (Mirabelli 1982, Ciaccio *et al.* 1989, Massa *et al.* 1991, Yosef 1991, Goodman and Haynes 1992, Kemp 1993, Morimando *et al* 1997, Jenkins and Avery 1999, Stephenson 2001, Grenci e Di Vittorio 2004, Souttou *et al.* 2005, De Sanctis *et al.* 2009). Levins' standardized formula: $B_A = B - 1/n - 1$ where $B = 1/\Sigma\ pi^2$ (Jenkins and Avery 1999)

falcon parents have a need to feed chicks that are becoming larger with an ever-increasing requirement for additional nutritional intake (Kemp 1975). In these circumstance, a variable niche in dietary breadth could be expected. Figure 7.4 shows this variability in relation to breeding stage and chick age in the data from eastern Sicily. The maximum peak occurred in April when all breeding pairs are involved in rearing young of various ages (Figure 7.4). A strong decrease later in the season coincides with the fledging period but some pairs that have bred late were still engaged in feeding young at the nest (Figure 7.4). During June and July, birds without parental duties seem to enlarge and vary their diet, resulting in a higher value for the index

FIGURE 7.2 The percentage proportions of different prey classes (birds, mammals, and reptiles) present in the diets of Lanner falcons in various locations (Mirabelli 1982, Ciaccio *et al.* 1989, Massa *et al.* 1991, Yosef 1991, Goodman and Haynes 1992, Kemp 1993, Morimando *et al* 1997, Jenkins and Avery 1999, Stephenson 2001, Grenci e Di Vittorio 2004, Souttou *et al.* 2005, De Sanctis *et al.* 2009)..

which is probably as a result of the inclusion of alternative prey (Figure 7.4).

Frequency and biomass

Quantitative analysis reveals a great deal of information with regard to the relative importance of certain prey groups and species in terms of both frequency and biomass. In Abruzzi in central Italy, birds accounted for 95.4% of Lanner falcon prey, and mammals 4.6% of total biomass (De Sanctis *et al.* 2009). The five most common prey species are Pigeons, Magpies, Jays, Woodpigeons, and Jackdaws but a very large proportion of prey by biomass is accounted for by Woodpigeon which make up 22.1% of the total (De Sanctis *et al.* 2009). In Sicily the main prey species are Magpies, Rock and Feral pigeons, Spanish Sparrows *Passer hispaniolensis*, Starlings (both Spotless and Common), and Jackdaws (Massa *et al.* 1991). In this case, the diet by frequency consisted of 52% birds, 44% arthropods, 2.8% mammals, and 1.2% reptiles (Ciaccio *et al.* 1989). However, prey by biomass is almost entirely accounted for by bird species which make up 98% of the total (Grenci and Di Vittorio 2004).

In the desert regions of the Negev highlands, *Alectoris chukar*, *Pterocles* sp., and *Columbia livia* constitute the bulk of the diet of Lanner falcons (Yosef 1991). Lanner falcons in these regions also preyed on rodents from a perch, or gathered invertebrates directly from the ground (Yosef 1991). In the Darb el Arba' desert of the Eastern Sahara, *Coturnix coturnix* and *Streptopelia turtur* made up 34% and 19% respectively of the total biomass consumed (Goodman and Haynes 1992). In this region, Lanner falcons that start to breed in mid-February are synchronised with the migratory cycle of their main prey and are therefore able to feed their nestlings on birds that are passing through between late March and early May (Goodman and Haynes 1992). Any late breeding attempts presumably face a prey shortage in the second half of the nesting period (Jany 1960, Goodman and Haynes 1992). In the early portion of the breeding season adults also feed extensively on locusts (Goodman and Haynes 1992).

In central-southern Algeria, rodents constitute the bulk of the diet (55.9%), followed by insects (22.5%) and arachnids (15.5%), birds (4%), reptiles (1%), insectivores (0.9%), and amphibians (0.2%) (Souttou *et al.* 2005). Rodents are also the main prey by biomass (83.4%), followed by birds with 12.1%, and other groups which together amount to 2.1% (Souttou *et al.* 2005). *Gerbillus gerbillus* is the most common species to be preyed upon by the Lanner falcon in this area making up 63.6% of the total, while *G. pyramidum* is second accounting for 14.4%, followed by *Pachyuromys duprasi* at 5.3% and *Jaculus jaculus* at 2.4% (Souttou *et al.* 2005). In terms of biomass, *G. gerbillus* is the most abundant prey species making up 57.9% of the total (Souttou *et al.* 2005). *Gerbillinae* sp. and *G. pyramidum* make up 15.8% and 15.1% of the total biomass respectively, followed by *Pachyuromys duprasi* at 7.1% and *Jaculus jaculus* at

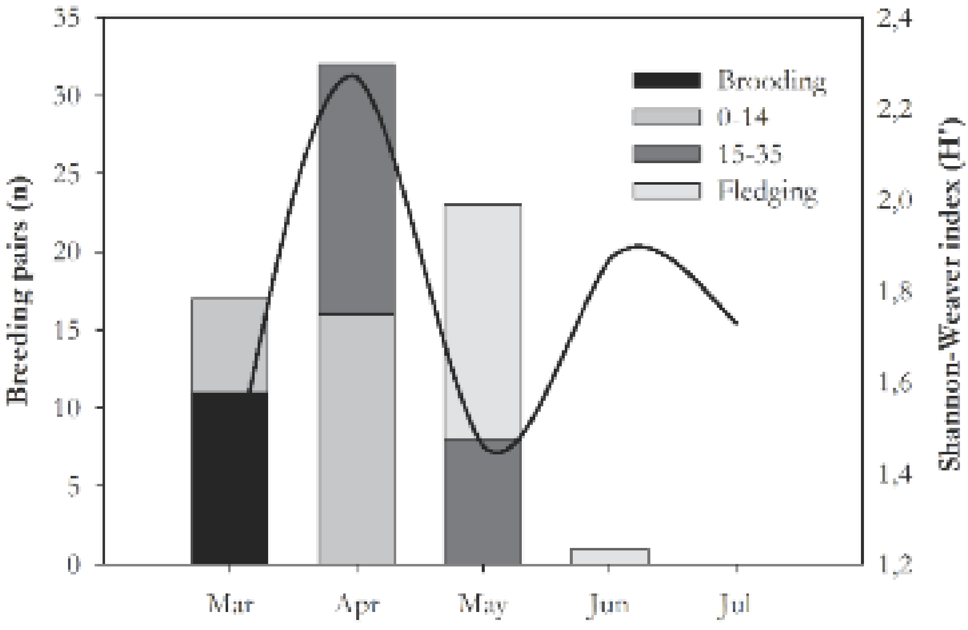


FIGURE 7.4 Variability in dietary breadth of the Lanner falcon (using the Shannon-Weaver index) in relation to breeding phase and age of chicks. Foraging index was collected by Ciaccio *et al.* (1989) and breeding data by Leonardi *et al.* (unpubl. data) in the same sample area in eastern Sicily.

4.1% (Souttou *et al.* 2005).

In the Air massif along the Chad–Niger border, prey remains included birds such as *Streptopelia turtur*, *Columba livia*, passerines, small mammals including *Gerbillus* sp. and *Jaculus jaculus*, reptiles including lizards and a small snake, and invertebrates including *Galeodes* sp. spiders, large numbers of *Coleopterae* and a dozen scorpions (Newby 1981). In Marrakech in Morocco, the diet of the Lanner falcon is made up of small birds and mammals including *Meriones shawi* and larks (*Galerida* sp.), mammals such as *Gerbillus campestris* and *Mus spretus*, and insects (Barreau and Bergier 2001).

In Eastern Cape Province, the diet of Lanner falcons was made up of 20% domestic chickens, 10% Rock pigeons, 9% Red-eyed Doves, and 7% Speckled Mousebirds (Stephenson 2001). The remains of domestic chickens that were found in the diet of these birds were aged about three weeks old, and it is probable that larger individuals would be too heavy for a Lanner falcon to lift into the air and carry off (Jenkins and Avery 1999, Stephenson 2001). Similarly, in the Soutpansberg area, Lanner falcons also took domestic chickens, which accounted for 40% and 30% of their diet, by frequency and biomass respectively. Doves accounted for a further 20% and 25%, by frequency and biomass, and Crowned Plovers *Vanellus coronatus* for 9% and 12 % (Jenkins and Avery 1999).

In one study, a high proportion of the remains recovered from the nests of Lanner falcon were of young chickens, and these *juvenile* birds accounted for 39.7% of the total identified prey (Jenkins and Avery 1999). Interestingly, such sources of free-ranging poultry could only be found at a considerable distance from the studied Lanner falcon nest sites, and their frequency in prey remains suggests that the hunting ranges of the falcons extended more than ten kilometres from their nest (Jenkins and Avery 1999). Terrestrial or cursorial species tended to dominate the diet of the Lanner falcons studied at Soutpansberg, and most prey were probably taken on, or close to, the ground (Jenkins and Avery 1999).

7.3 Other avian prey

Falco biarmicus feldeggii

Lanner falcons, especially male birds, frequently hunt Eurasian Crag Martins *Ptyonoprogne rupestris* and *Hirundo* sp. (80% of prey) during the fledging period in Calabria (Mirabelli 1982). The Jackdaw *Corvus monedula* is also successfully hunted at Sigri Castle in Greece as well as Little Bittern *Ixobrychus minutus* in Faneromeni, Lesvos in Greece (Dudley 2010). W. Baumgart, quoted in Boev and Dimitrov (1995), reported attacks by Lanner falcons on Alpine Chough *Pyrrhcorax graculus.* Rock pigeon *Columba livia* is also to be the main prey species in Crete (Dresser 1871-1881). In July, numerous species of small birds are preyed on by Lanner falcons at Dogubayazit in eastern Turkey, and Jackdaws and Crows *Corvus corone cornix* at Mugla (Aegean Sea, Turkey). Small birds were found in prey remains at nest sites in Georgia (Abuladze 2013) and Blackbirds *Turdus merula* are preyed upon by Lanner falcons in Bulgaria.

Falco biarmicus erlangeri

In common with *F. b. biarmicus* and *F. b. abyssinicus*, this race feeds its young with chicks in Tunisia, Algeria (at Tlemcen), and Morocco (Bergier 1987, Azafzaf 1999). In addition, *F. b. tanypterus* take Barbary Partridge *Alectoris barbara* as prey (Azafzaf 1999). Pigeons *Columba* sp. are hunted at Oued Massa in Morocco, and at Nouakchott one Lanner falcon was found with a dead pigeon *Columba livia* (P.W.P. Browne pers. obs., Bergier 1987). The remains of a Turtle Dove *Streptopelia turtur* was found in pellets at Serir Tibesti in Libya (Jany 1960). At the same site, pellets were also found to contain *Motacilla flava*, Quail *Coturnix coturnix*, and Hoopoe *Upupa epops* (Jany 1960). Lanner falcons were observed attacking a flock of over a hundred Spotted Sandgrouse *Pterocles senegallus* at Gleb Jdiane in Morocco (Bergier *et al.* 2013). *F. b. erlangeri* also hunts Wheatears *Oenanthe* sp. feeding on their semi-arid wintering areas in eastern and southern Morocco, and Black-eared Wheatear *Oenanthe hispanica* in southern Algeria. Lanner falcons also hunt Yellow Wagtail *Motacilla flava* at Khnifiss in Morocco and *Motacilla* sp. in Algeria (Bergier *et al.* 2013).

Migratory birds such as Common Starling *Sturnus vulgaris* and Song Thrush *Turdus philomelos* are regularly hunted by Lanner falcons during their migratory passage through northern Tunisia (Azafzaf 1999). A group of Desert sparrows *Passer simplex* was attacked by an immature male Lanner falcon around 100 kilometres from Awserd in Morocco (Bergier *et al.* 2013). Other passerine species that are hunted include Sardinian warbler *Sylvia melanocephala* which was hunted at Iwik (Banc d'Arguin, Mauritania), House sparrow *Passer* sp. which is regularly hunted in Morocco (Bergier 1987), and Barn Swallow *Hirundo rustica* which was hunted at the oasis of Ouadâne in Mauritania. Lanner falcons will also hunt Hoopoe *Upupa epops*, and Meadow pipit *Anthus pratensis* in Morocco, as well as Common redstart *Phoenicurus phoenicurus* in Algeria (Bergier 1987).

Among wader species, Common sandpiper *Actitis hypoleucos* is hunted in Morocco, Common Redshank *Tringa totanus* at Lake Mansour Eddahbi in Morocco, and *Tringa glareola*, *Tringa totanus*, and *Calidris alpina* at Banc d'Arguin in Mauritania. A Lanner falcon was also seen to attack a Great Cormorant *Phalacrocorax carbo* at La Janda, Cádiz (S. Daly pers. obs.) and an unidentified species of small wader at Playa de los Lances (Tarifa, Cádiz, Spain).

Falco biarmicus tanypterus

The Eurasian Blackcap *Sylvia atricapilla* is hunted by Lanner falcons at dusk from their night roost at Khartoum in Sudan (Butler 1905). Wagtails *Motacilla* sp. are also attacked in Sudan usually as they are returning to their roost site in date-palms about half an hour after sunset after having travelled a great distance up the White Nile during the day in search of prey (Butler 1905). Greater short-toed larks *Calandrella brachydactyla* are hunted at Manifa, Saudi Arabia, and Pipits at Mount Carmel in Israel. There are reports of Hoopoe *Upupa epops* being captured by a Lanner falcon at the Great Pyramid in Egypt, and of Feral Pigeons *Columba livia* being pursued in flight at Sinai, Egypt (Wyatt 1870). Prey attacked in Oman include Sandgrouse *Pterocles* sp. and various small birds are hunted in the area of the St. Katherine monastery in Egypt (Meakin *et al.* 2005). Ringed Plover *Charadrius hiaticula* was seen to be captured on the ground at Khartoum in Sudan, and a flock of six birds of *Tringa* sp. were hunted by a Lanner falcon at the Qara oasis near the Qattara depression in Egypt (Butler 1905). The bulk of the prey taken by Lanner falcons in Israel is made up of Rock Doves, Quails, Jackdaws, Plovers, and sometimes Teal *Anas crecca*.

Falco biarmicus abyssinicus

Unfortunately no quantitative data exist on the dietary preferences of this race. From the analysis of stomach contents, prey in Senafé in Eritrea and in the former Shewa region of Ethiopia seems to be predominantly small birds (Salvadori 1884). In Arada in Chad, Crested lark *Galerida cristata* and probably *Streptopelia senegalensis* were observed being brought to young in the nest by Lanner falcons (Newby 1979). Lanner falcons have also been observed hunting Turtle doves *Streptopelia turtur* through perch-hunting at a water hole in the Tibesti massif in Chad (Simon 1965). Species of Larks and Weaver birds *Ploceidae* sp. are hunted in Gambia (Gore 1981) and Wheatears *Oenanthe* sp. are hunted on their semi-arid wintering areas in eastern Eritrea. Lanner falcon prey identified at the Ouadi Rimé-Ouadi Achim Faunal Reserve in Chad includes Guineafowls, Francolins, Plovers *Charadrius* sp., small waders, Little stint *Calidris minuta*, and Ringed Plover *Charadrius hiaticula* (Newby 1979).

White-collared pigeon *Columba albitorques* was hunted by Lanner falcons while feeding in Erica forest near cliffs in the Abune Yosef Massif of Ethiopia. Speckled pigeons *Columba guinea* were preyed on in Dakar, Senegal. In common with *F. b. biarmicus*, *F. b. abyssinicus* also frequently feeds on domestic poultry, in the Gabù region of Guinea-Bissau for example (G. Carron pers. comm.), as well as in Iju (Nigeria) and in Ghana (Dowsett-Lemaire and Dowsett 2014). Lanner falcons are also known to hunt birds in wetlands and coastal zones, such as Common teal *Anas crecca* which they prey on during breeding season at Bishoftu in Ethiopia, various wader species in Ghana, and Crab Plover *Dromas ardeola* at its breeding colonies in the Dahlak Archipelago of Eritrea (Guichard 1950, Dowsett-Lemaire and Dowsett 2014).

At times of year when they are readily available, *F. b. abyssinicus* exploits large quantities of small passerines such as Barn Swallow and Red-billed Quelea. They frequently feed on Barn swallows *Hirundo rustica* at their roosts in the Afi Mountains in Nigeria (Bijlsma and van den Brink 2005). Red-billed Quelea were observed being hunted in early August at Agoufou in Mali, and sometimes a pair of Lanner falcons were observed hunting these together. *F. b. abyssinicus* could be expected to have a major impact on the breeding performance of Red-billed Quelea colonies in Mali due to an average success rate of 10% in hunts by *juvenile* and adult Lanner falcons (Thiollay 1975).

An attempt by a Lanner falcon to attack a particularly large prey species in the form Saviles Bustard *Lophotis savilei* is recorded from South Sudan (Lynes 1925).

Falco biarmicus biarmicus

A large quantity of data are available on the feeding habits and prey selection of *F. b. biarmicus* scattered across the published literature. It is noted for frequently attacking domestic poultry in South Africa, Zimbabwe, Tanzania, and Zambia until this stable and easy food source becomes locally depleted (Barbour 1971, Irwin 1981, Brown *et al.* 1982, Dowsett *et al.* 2008). The preferred chickens were about pigeon'-sized and the Lanner falcon often struggled to fly off with the '*loot*' (A. M. Muller pers. comm.). Having successfully carried off its kill, the Lanner falcon often returned to its perch site on a branch at the top of a of Baobab tree in order to pluck the chicken, as has been observed at Morogoro, in Tanzania.

Pigeons *Columba livia*, quails, partridges and *Streptopelia* sp. doves are some of the main prey species that are favoured by Lanner falcons in urban areas such as Durban, Cape Province, and Magaliesberg in South Africa, and in Zimbabwe (Sharpe 1904, Finch-Davies 1920, Craib 1977, Irwin 1981, Steyn 1983, Mendelsohn 1988). The Laughing Dove *Streptopelia senegalensis* is recorded as a prey species in Zambia (Benson *et al.* 1971).

Larks are hunted by Lanner falcons in the Kalahari desert of Namibia (MacLean 1970), Black-cheeked Lovebirds *Agapornis nigrigenis* frequently attacked at waterholes in Zambia, and Blacksmith Plovers *Hoplopterus armatus* in flocks at Cape Town in South Africa. In the Eastern Cape region of South Africa, Pied starlings *Spreo bicolour* and Redwinged starling *Onychogonathus morio* suffered from the predation of several of their nestlings by a Lanner falcon (one success out of three attempts) on subsequent days (Zyl, van 1991). African starlings *Onychognathus* sp. and Masked Weaver *Ploceus velatus* were also attacked by continuous swoops on single individuals by Lanner falcons. Repeated stoops were also used for capturing a Pied kingfisher *Cerlyle rudis* at the Albert Falls Dam in South Africa. The bird subsequently took to the ground exhausted where the Lanner falcon could then easily catch it (Porter 1982). An adult Lanner falcon was shot with a Kingfisher in its talons at Morogoro in Tanzania.

In South Africa, Lanner falcons hunted Crowned guineafowl *Numida meleagris* (Grobler and Braack 1984), and very large prey such as the Black-bellied bustard *Lissotis melanogaster*, by dive-bombing them in long grass and then catching them when they try to escape in a crouched posture (Swardt, de 2006). The Striped Flufftail *Sarothrura affinis* is also recorded as a prey species in South Africa, and Lanner falcons have been known to seize African Grey Hornbill *Tockus nasutus* and Yellow-billed Hornbill *Tockus leucomelas* in Zambia, which it seems it was unable to lift (Benson *et al.* 1971, Steyn 1983). Lanner falcons have also been recorded feeding on Yellow-billed hornbill as carrion (A. M. Muller pers. comm.). In addition, Trumpeter Hornbill *Bycanistes bucinator* and Silvery-cheeked Hornbills *B. brevis* (Barnard 2015) have been recorded as prey species.

The Lanner falcon is capable of capturing fast prey such as Mottled Swifts *Tachymarptis aequatorialis* using a 'sit-and-wait' ambush technique near the entrance of the colony in Zimbabwe (Cooke 1965). It will also occasionally take Little Swift *Apus* *affinis* in northern Zambia (Brooke and Vernon 1961). European Swallows *Hirundo rustica* are also often hunted at roosts, such as in Botswana for example (Steyn 1983, Bijlsma and van den Brink 2005). In urban areas, such as Johannesburg and Durban in South Africa, the favoured prey species are Feral pigeon, *Streptopelia senegalensis*, *Streptopelia semitorquata*, *Philomachus petrosus*, and *Pluvialis squatarola* in Durban and also other species of small birds in Harare (Kellow-Webb and Dingley 1972, Sinclair and Walters 1976, Tarboton and Allan 1984).

Among other prey species, the Cape Parrot *Poicephalus robustus* is occasionally taken, especially by young birds in South Africa, the Black-headed Oriole, and Orange-throated Longclaw which are hunted at their roosts, as well as *Colius* sp. in Kenya and Red Bishop at Magaliesberg (Jackson 1938, Steyn 1983). The Red-billed Quelea is a favourite prey, especially for immature birds where huge flocks are often concentrated at water-holes in Kenya and Namibia (Britton 1980, Steyn 1983). Species of Sandgrouse are also often hunted at waterholes including Namaqua Sandgrouse *Pterocles namaqua* in South Africa, and Black-faced sandgrouse *Pterocles decorates* in Kenya.

Among wader species, *Calidris minuta* is occasionally predated at the South Western Cape, and Lanner falcons have also been known to hunt Grey Plover, Crowned Plover, and Ruff (A. M. Muller pers. comm., Steyn 1983).

7.4 Other Mammalian prey

Falco biarmicus feldeggii

An analysis of prey remains showed that all of the European Rabbits found in the diet of the Lanner falcons in Sicily were young animals, perhaps caught using low-level flights (Massa *et al.* 1991). The remains of Common Vole *Microtus arvalis* were found under a power pylon at Magaro in the Kakheti Region of Georgia, at a site known to be used by Lanner falcons (Abuladze 2013).

Falco biarmicus erlangeri

In the desert areas of southern Tunisia and Algeria, several species of small mammals are readily available and easy for Lanner falcons to catch, including *Ctenodactylus gundi*, *Psammomys obesus*, and *Elephantulus rozeti* (Azafzaf 1999). In the Guelmin desert area of Morocco, a group of at least twenty Lanner falcons were observed feeding on *Psammomys obesus* (Figure 7.5; Laidi *et al.* 2012), and five Lanner falcons were observed taking advantage of an abundance of Fat Sand Rats in Tan Tan in Morocco (Bergier *et al.* 2013).

In Serdeles at Western Fezzan in Libya during May, a pair of Lanner falcons were

Figure 7.5 Fat-tailed Sand rat *Psammomys obesus*, frequently preyed upon by Lanner falcons in desert areas when it is locally abundant, attracting several *F. b. erlangeri* individuals. © and courtesy of Stig Frode Olsen.

observed beginning to catch Trident bats *Asellia tridens* at around 18:45 and they continued to hunt bats until 19:30 (Jany 1960). A pair of Lanner falcons in the mountain oasis of Chebika in western Tunisia were said to feed '*nearly exclusively*' on bats during the twilight period when bats tend to leave their roosts (Azafzaf 1999).

The remains of Hedgehogs were associated with Lanner falcons at Oued Nea in the M'Zab area of Algeria (Hartert 1915). Among the *Soricidae* family, Whitaker's Shrew *Crocidura whitakeri* is a rare prey species for the Lanner falcon (Souttou *et al.* 2005). At a nest site with young in the Western Desert of Morocco the remains of many Orthopters and a Hare *Lepus* sp. skull were found (Bergier *et al.* 2013).

Falco biarmicus tanypterus

In common with other Lanner falcon populations in north Africa and Israel, *F. b. tanypterus* is known to hunt *Psammomys obesus* (Yosef 1991). An attack on *Lepus capensis* by a trained Lanner falcon was recorded by C. Tristam, quoted in Langford (1912) and a female *F. b. tanypterus* was seen in flight in Israel with a hare in its talons, but it is possible that this was a scavenged road kill (Yosef 1991).

In Israel, the species of bat hunted by Lanner falcons includes European free-tailed bat *Tadarita teniotis* and Kuhls Pipistrelle *Pipistrellus kuhlii* (Yosef 1991). A pair were also observed hunting an unidentified species of bat at a quarry near the Meroe Pyramid at Khartoum in Sudan (Butler 1905).

Falco biarmicus abyssinicus

In the Simien and Bale Mountains of northern Ethiopia, Lanner falcons feed on the abundant small rats *Arvicanthis* sp. using high speed flights low over the ground (Brown *et al.* 1982).

In Aden, *F. b. abyssinicus* hunts small fruit bats that it captures at dusk by waiting in pairs near the entrance of the cave where the bats roost. Large numbers of bats fly out shortly after dusk and are promptly pounced on by one or other of the waiting falcons. Fruit bats are also hunted in Liberia and Wahlbergs Epauletted fruit bat *Epomophorus wahlbergi* in central east Africa (Gatter 1997).

Falco biarmicus biarmicus

Groups of ten or more *juvenile* Lanner falcons have been observed congregating with Steppe buzzards, Black-breasted snake-eagles, and Booted eagles when fallow fields were being ploughed and rats were often left exposed (A. A. Muller pers. comm.). Any movement was pounced on by the buzzards and eagles, and the Lanner falcons either snatched up the rats directly from the ground or stole them from the other raptors (A. A. Muller pers. comm.).

Small mammals were also found in the stomach contents of Lanner falcons in Newcastle in South Africa, and are counted amongst the prey species of urban Lanner falcons in Harare in Zimbabwe (Kellow-Webb and Dingley 1972). Species of *Rhabdomys* sp. mice were exploited at rubbish dumps at Cape Province in South Africa (Pitman 1967).

Fruit bats *Eidolon* sp. are hunted in eastern Africa and many successful captures of Egyptian fruit bat *Rousettus aegyptiacus* in flight have been observed in the Cape region of South Africa (Jacobsen and du Plessis 1976). Unidentified species of bats were also present in the diet of Lanner falcons at urban sites in Durban, Harare, and Johannesburg (Kellow-Webb and Dingley 1972, Nichols and Campbell 1978, Thomsett 1987). In Kenya, bats belonging to both *Microchiroptera* sp. and *Macrochiroptera* sp., including Lesser leaf-nosed bat *Hipposideros caffer*, Yellow-bellied bat *Scotophilus nigrita*, and Flat-headed free-tailed bat *Sauromys petrophilus*, have been associated with hunting Lanner falcons (Thomsett 1987).

In common with *F. b. feldeggii*, *F. b. biarmicus* may also prey on the domestic cat in South Africa (Langford 1912). Perhaps employing an opportunistic hunting technique, a pair of Lanner falcons were observed hunting near a cat that was searching for rats in open terrain in Natal, South Africa (Gurney 1860).

7.5 Reptiles and Amphibians

Falco biarmicus feldeggii

In Calabria, Lanner falcons are known to feed on small snakes and lizards but they do not consume the entire animal, possibly due the flesh being somewhat unpalatable to the birds (Mirabelli 1982). Mebs (1959) found a Toad *Bufo bufo spinosus* taken as prey in Sicily and a similar finding from a site in north-eastern Sicily was probably recovered as carrion after having been killed on a road (Leonardi 2001).

Remains of lizards have also been reported from nests in Georgia (Abuladze 2013).

Falco biarmicus erlangeri

In the deserts of north-west Africa, the Lanner falcon takes large Bells Dab Lizard *Uromastyx acanthinura* taking advantage of swift flights over level ground in order to seize prey (Heim de Balsac and Heim de Balsac 1954). This species has also been found in the stomach contents of Lanner falcons at Oued Nea in the M'Zab area of Algeria, and at Zemmour in Morocco (Hartert 1915, Bergier 1987). Bell's Dab Lizard are also used for feeding young, behaviour which has been observed in Mauritania where a number of lizard tails were found under a tree nest or in the area around a ground nest (Figure 5.11; Salewski and Martignoli 2005). In the western desert area of Morocco, Bibron's Agama *Agama impalearis* has been found in the stomach contents of Lanner falcons (Bergier 1987). A pair in Oued Sbaihia/Zanghouan has also been observed feeding snakes to their young (W. Suetens), and in southern Tunisia chicks are fed lizards (Azafzaf 1999).

Falco biarmicus tanypterus

Reptiles are known to be part of the diet of the Lanner falcon in Israel, and there have been reports from Egypt of a small green snake captured on the ground at El Amarna.

Falco biarmicus abyssinicus

Skinks of the *Scincidae* group have been observed being fed to young Lanner falcons in a nest at Arada, in Chad (Newby 1979), and observers watched a Lanner falcon catch and devour a large lizard in Ethiopia (Ogilvie-Grant and Reid 1901).

Falco biarmicus biarmicus

During road surveys in the Cape Province of South Africa, Lanner falcons were observed feeding on *Psammophis* sp. of colubrid snakes as well as *Chamalaeleo namaquensis* (Pitman 1967).

7.6 Invertebrates

Falco biarmicus feldeggii

A number of individuals are regularly seen feeding on swarms of locusts for periods of many days over the steppe-like pasturelands of the Gargano peninsula (Caldarella *et al.* 2005). In Sicily, the stomach contents of a *juvenile* Lanner falcon was found to contain twenty ants. In the National Park of Calabria in Southern Italy, two adults and three *juveniles* were observed together, hunting flying insects in the air above clearings on the slopes on the 3rd of July (V. Škorpíková pers. comm.).

However, a careful inspection of Lanner falcon pellets showed that most of the insects found came from the insides of the gizzard remains of other prey species such as Green Woodpeckers and Starlings (Morimando *et al.* 1997).

Falco biarmicus erlangeri

The remains of Orthopteran prey were found at a nest site with young in the western desert region of Morocco (Bergier *et al.* 2013). During periods when the insects are found in swarms in Morocco, the Lanner falcon feeds on African desert locusts *Schistocerca gregaria* and Grasshoppers *Acrididae*. Remains of locusts were also found in the stomach contents of Lanner falcons in central Tunisia (Erlanger 1898). In central-southern Algeria, insects and arachnids account for a sizable proportion of the entire diet of Lanner falcons, accounting for 22.5% and 15.5% respectively (Souttou *et al.* 2005). Orthoptera, Coleoptera, and *Tenebrionidae* were recovered from pellets at El Ayoun in the Western Desert.

Falco biarmicus tanypterus

This race has been known to feed on locusts and crickets in Israel, and the remains of locust exoskeletons are also relatively commonly associated with Lanner falcons sites (Goodman and Haynes 1992). However, all prey remains found in the Eastern Desert were of migratory birds.

Falco biarmicus abyssinicus

In south-eastern Niger, Lanner falcons grab flushed grasshoppers in mid-air, and up to four individuals can commonly be seen feeding together with Storks (Jensen *et al.* 2008). In Mali and Mauritania, they also feed on desert locusts alongside other raptors such as Black Kites (Sanchez-Zapata *et al.* 2007). Lanner falcons have been observed catching and handling desert locusts on the wing at Bishoftu, in Ethiopia (Guichard 1950). A *juvenile* was found to have nine desert locusts in its crop and fifteen in its stomach at Debaroa (6,400 metres above sea level) in Eritrea (Smith and Popov 1953). Also in Eritrea, thirteen gorged birds were found in a two-hectare field after feeding on swarms of termites (Ash and Atkins 2009). Lanner falcons are also known to feed on flying termites in Gambia (Figure s40; Gore 1981).

Falco biarmicus biarmicus

Locusts, grasshoppers, beetles, and termites are the main invertebrates prey of Lanner falcons in southern Africa (Langford 1912, Steyn 1983). Grasshoppers and locusts were mostly eaten outside the breeding season, when adult and *juvenile* Lanner falcons were seen stalking these insects on foot in short grass and in pastures that had been recently cut (Stephenson 2001). It seems that insects such as flying ants and termites may be the most common prey taken by recently-fledged Lanner falcons because they are easy for the birds to capture. A group of fifteen *juveniles* and five adults were seen feeding on large numbers of flying termites *Hodotermes mossambicus* in the Karibib district of Namibia (Jensen 1972). Whenever there is a termite emergence after a thunderstorm, Lanner falcons do not hesitate to catch them, and consume the termites while on the wing (Stephenson 2001). The Lanner falcon also feeds on termite swarms during influxes into the arid Tsavo East National Park, Kenya during the wet season in November–March (Lewis and Pomeroy 1989). Lanner falcons catch large flying insects at the 2,450 metre high Ruhinda Ridge in Uganda, and prey on locusts in south-western Tanzania (Vesey-FitzGerald 1955). From the examination of stomach contents, it seems that Lanner falcons prey on grasshoppers at Newcastle (South Africa), Orthoptera at Chibale (Zambia), and locusts at the Eldama ravine (Kenya).

7.7 Differences with the Peregrine

There is a degree of quantitative and qualitative overlap in the diets of Lanner and Peregrine falcons in Sicily (Sorensen index: L = 0.56; P = 0.59; Ciaccio *et al.* 1989). However, cluster analyses on diet composition showed a clear separation between *F. p. minor* and *F. b. biarmicus* sites (Jenkins and Avery 1999). The analysis showed that inter-specific dietary overlap was greatest between pairs with close neighbouring congeners (Jenkins and Avery 1999). There was a significant difference in the foraging habitats used by Peregrine and Lanner falcons in the Soutpansberg area, as in-

FIGURE S48 *F. b. abyssinicus* hunting termites in flight in the Gambia. © and courtesy of Dave Montreuil.

FIGURE S49 Predator, a *juvenile F. b. biarmicus*, and prey, *Streptopelia capicola*, share the same tree (Kgalagadi Transfrontier Park, South Africa). © and courtesy of Brett E. Ellis.

ferred from the habitat preferences of their prey (Jenkins and Avery 1999). While both species favoured the wooded plains below the mountain range, Peregrine falcons took more woodland species from relatively undisturbed habitats, whereas Lanner falcons tended to prefer more open-country species from denuded woodland and free-range chickens from around human settlements (Jenkins and Avery 1999).

7.8 Hunting techniques

A variety various hunting techniques are used by the Lanner falcon due to the morphological traits that allow various styles of flight (see also section 2.5; Jenkins 1995). A quantitative study by Jenkins (1995) reported a success rate of 22.6% of total strikes, where 85.5% were perch-hunts and 14.5% were aerial hunts. Hunts frequently consist of cooperative attacks (43.5%), and less often of attempts at flushing prey from cover (6.5%; Jenkins 1995). The majority of prey is caught in the air (90.3%), and on only a few occasions were prey taken on the ground or on a cliff face. These were either initially struck in the air and retrieved from the ground, or initially chased out of cover on the ground (Jenkins 1995). Although these percentages relate to the nominate race *F. b. biarmicus*, it is likely that the other subspecies follow a similar pattern despite some variations in relation to local conditions. In a study of hunting by *F. b. tanypterus*, out of a total of 332 hunting attempts on birds, mammals, and insects, 49% were successful (Yosef 1991) and in 83% of observations the prey was caught in flight (Yosef 1991). Interestingly, males seemed to be less successful than their mates, although cooperative hunting between the pair enhanced hunting success (Yosef 1991). In addition, females had greater success than males when hunting cooperatively with young (Yosef 1991).

F. b. feldeggii is capable of snatching prey such as Starling that is perched on cliffs and trees, and will also attempt to grab Pigeons or Jackdaws inside their nests (Mebs 1959, Ciaccio *et al.* 1989). *F. b. erlangeri* hunts *Psammomys obesus* in Morocco during periods of particularly high densities in December, along with a number of other raptor species including *Aquila chrysaetos* and *Buteo rufinus*, as well as mammals such as *Felis sylvestris lybica* (Figure 7.5; Laidi *et al.* 2012). In Banc d'Arguin in Mauritania, hunting was centred on a wader roost and was dependent on the tidal cycle, with most hunting taking place during the 1–2 hours of high tide (Bijlsma 1990). The Lanner falcons started hunting as soon as the waders had to leave their feeding areas because of the incoming tide and started to flock at pre-roost gatherings (Bijlsma 1990). The Lanner falcon has been reported breeding on the remote islands at Banc d'Arguin, where eggs are laid between early February and early May, and fledging takes place between early April and early May (van den Hout 2010). There is therefore a danger that terrestrial predators, such as the Golden Jackal *Canis aureus*, will take eggs or the incubating parent, which coincides with times when shorebirds become more vulnerable to predation as they fuel up for their migration northwards (van den Hout 2010). Hovering, in the manner of the Eurasian Kestrel, has been observed in Lanner falcons in Sicily and Greece, although only rarely (Ciaccio *et al.* 1989, Massa *et al.* 1991). In Israel, during late summer and autumn (mid-June to late November), mates are most often seen hunting separately and feeding alone (Yosef 1991).

Hunting from perches

When hunting from a perch, the Lanner falcon will typically spot prey, leave the perch and drop down low in order to generate speed just above the ground in the direction of the sitting prey (A. M. Muller pers. comm.). Usually the prey will catch sight of the attacking falcon and try to escape and the falcon will then attempt to catch the prey in mid-air as it takes flight (A. M. Muller pers. comm.). Prey species hunted in this fashion include *C. livia*, *C. guinea*, Red Bishop, and other small birds, but also larger prey such as Red-billed Quelea and Sandgrouse (Kemp 1993, A. M. Muller pers. comm.). Attacks can take place across distances of up to 1,500 metres and be launched from a height of 25 metres from the top of electricity pylons (Kemp 1993). One such attempt was on a Laughing Dove, which was successfully caught by an adult male which had been incubating at a nest site on a pylon (Kemp 1993). Although perched Lanner falcons often make repeated attacks from a perch site on a pole, success rates are often low (Kemp 1993, Stephenson 2001). No observations have been made of Lanner falcons initiating hunts directly from nest sites on cliffs (Stephenson 2001).

Foraging strategies at water holes

In very arid environments Lanner falcons often take advantage of prey that use water holes for drinking by foraging around this type of site. Namaqua Sandgrouse *Pterocles namaqua*, Burchell's sandgrouse *Pterocles burchelli*, Speckled Rock Pigeon Columba guinea, Cape Turtle Dove *Streptopelia capicola*, Laughing Dove *Streptopelia senegalensis*, and Namaqua Dove *Oena capensis* are the main prey species that are hunted in this way (Figure 7.1). These species come to water holes in order to drink and wet their feathers, which are typically brief acts that require no more than 10 to 15 seconds for completion after the water is reached (Cade 1965). When a group of doves left their perches in Acacia trees and set their wings to glide down towards the water hole, the hunting Lanner falcon will stoop from high perches in Acacia trees or from a circling position over a nearby river (Cade 1965). The behaviour of five columbiform species at the Gobabeb water hole suggests that these birds are most vulnerable to capture while actually at the water drinking, as well as when they are approaching or leaving the water across the open bed of the river (Cade 1965). The Lanner falcon will sometimes manage to strike a bird down but will not always be successful in retrieving it (Cade 1965).

Attacks from soaring flight

A Lanner falcon hunting using this method will first soar to gain height and then launch attacks (Stephenson 2001). The majority of prey killed in this way, in around 63% of cases, were taken from a stoop, often after the falcon had been circling high (Yosef 1991). In 5% of cases, the falcon dropped below the prey and grasped it from below and behind (Yosef 1991). The Lanner falcon may also occasionally take avian prey '*head on*' by flying in the opposite direction (Brown *et al.* 1982). In Calabria, this technique is used with soaring flight lasting for more than fifteen minutes (Mirabelli 1982). Tracked Lanner falcons are frequently seen hunting in this manner, mainly preying on pigeons on passage or birds that had been flushed by sources of disturbance such as vehicles, cattle, and tractors working in fields (Stephenson 2001). After soaring in search of prey, stoops across distances of up to 1,200 metres were observed against a flock of Longtailed Widows *Coliuspasser progne* (Kemp 1993).

When it is pursuing small birds the Lanner falcon will descend from a great height with a succession of rapid twists (Gurney 1860). It will also take free-range poultry by swift attacks from sailing or soaring flight, often rushing at speed between trees and buildings (Brown *et al.* 1982). A Lanner falcon has been observed using a stooping flight to attack a flock of feral pigeons on the roof of a shed and one individual was successfully knocked down (A. M. Muller pers. comm.). Lanner falcons frequently strike prey down flying prey and they therefore tend to favour open habitats where fallen prey can be easily seen and retrieved from the ground (Jenkins 1994). Although it is mainly bird species that are hunted from stooping flights, Lanner falcons will also prey on flying termites that have emerged after a thunderstorm, although these are most often eaten by birds on the wing (Stephenson 2001).

Attacks from fast, low coursing flight

The most commonly observed hunting method was a single falcon coursing at low-level across the landscape at speed, trying to flush prey and chase it down (Stephenson 2001). This was mostly observed when a moderate to strong wind was blowing (Stephenson 2001). Adult Lanner falcons in flight should be more manoeuvrable due to their large wing area and long tail (Mirabelli 1982), and Lanner falcons will often make kills on the ground where there is very little margin for error. Species such as Stone Partridge *Ptilophachus petrosus* for example can be snatched in flight from a rock face after a swift near-vertical stoop of 300–400 metres (Brown *et al.*

1982). Other fast low-level attacks consist of a tenacious pursuit and short alternating stoops on escaping prey such as Dunlins *Calidris alpina* which seem to be particularly vulnerable to this form of attack (Bijlsma 1990). In Africa, Lanner falcons will use head-on flights to kill European Bee-eaters *Merops apiaster* which are travelling in the opposite direction.

Low-level surprise attacks are often aimed at targets at ground level such as Waders and Columbiforms (Figure 7.1). In one such attack, the Lanner falcon slowly circled a small flock of Redshanks *Tringa totanus*. The birds did not flush as a result of this slow stalk and one individual was simply picked up by the hunting falcon (Bijlsma 1990).

Cooperative hunting

When hunting cooperatively, the male Lanner falcon will usually flush and chase the prey in the direction of the female and the prey, upon detecting the female, will either turn back towards the male or continue flying directly into the path of the female (Yosef 1988, 1991). In one example, a pair of Lanner falcons attacked a flock of medium-large prey in the form of Rock pigeons from great height, one bird singled out a pigeon that was then caught by the second attacking falcon clinging to the wing of the pigeon (Figure 7.6). The prey was brought down, killed, and the falcon proceeded to feed (A. M. Muller pers. comm.). Although Mebs (1959) reported frequent vocalizations during cooperative hunting by pairs of Lanner falcons, a recent quantitative study found that there were no calls between the birds when they hunted together (Leonardi 1999).

During the latter half of breeding season, as well as after breeding has been completed, pairs often hunt together in this manner with a slight variation in that one falcon, usually the male, will often fly much higher than the other and the lower falcon will flush birds for the higher flying bird to stoop on (Stephenson 2001). *F. b. tanypterus* pairs have been known to hunt cooperatively during the courtship period prior to egg laying and also when young birds accompanied one of their parents on hunting forays (Yosef 1991). This form of cooperative hunting has been documented between an adult and *juvenile* Lanner falcon, with the adult doing the stooping, as well as with two *juveniles* hunting together (Stephenson 2001).

Only around 26% of cooperative attacks were initiated by female Lanner falcons, while the males initiated 74% of joint hunts (Leonardi 1999). Although males preferred to pursue larger prey (87%) and hunted larger flocks more often than females, male hunting success rates tended to be lower than those of females (Leonardi 1999). When prey was caught by the male, the female would take the kill and either return to the nest site with it or feed while the male perched nearby (A. M. Muller pers. comm., Stephenson 2001). In Sicily, females ate 70% of the prey captured in coo-

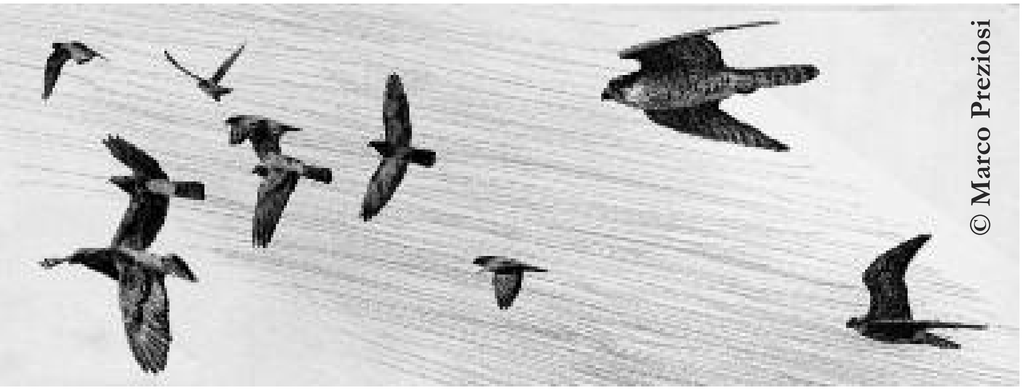


FIGURE 7.6 A pair of *F. b. feldeggii* hunting cooperatively in a flock of Rock pigeon. © and courtesy of Marco Preziosi.

perative hunts and males in 12% of cases fed on captured prey after the departure of the females (Leonardi 1999).

In fact, only 15% of total hunts were successful and but of those that were successful, the majority, around 50%, were through hunting cooperatively (Kemp 1993). Cooperative hunting is therefore usually more successful than hunting alone, and cooperative hunting between mates clearly enhances hunting success and the fact that it is practised most frequently prior to the breeding season suggests that it may be associated with pair bonding (Yosef 1991). Pairs have been observed hunting along a cliff, where one falcon would land and flush Rock pigeons and the other chased them (Stephenson 2001). Although Lanner falcons prefer to attack larger flocks, hunting success is inversely proportional to flock size when species such as Pigeons and Jackdaws are hunted (Leonardi 1999).

F. b. biarmicus hunts in pairs relatively frequently, and this may enable them to catch species such as Alpine Swifts which are too agile for individuals to catch easily on their own (Jenkins 1995). During hunting attempts directed towards Swifts, pairs of Lanner falcons will rise up together above the gorge on thermal updrafts and then stoop together, the female following the male fifty metres or so behind (A. M. Muller pers. comm.). Similarly in Sicily, cooperative hunting is frequently employed against Swifts *Apus apus*, with repeated stoops by both partners, or for hunting Rats *Rattus* sp. using low flights (Ciaccio *et al.* 1989, Massa *et al.* 1991).

In Banc d'Arguin in Mauritania, pairs of Lanner falcons hunted across wader roosts causing panic in the flock for several minutes until the male caught a Dunlin and left it to the female (Bijlsma 1990). This confusion and the associated dilution effect, had the effect of reducing hunting efficiency, and the Lanner falcons had difficulty in attempting to attack the group repeatedly, decreasing their overall success rate (Leonardi 1991). Similarly, *F. b. feldeggii* hunted Jackdaws using partial surprise attacks in 60.8% of cases. This method is employed much more frequently than non-surprise attacks, which were used in 21.6% of observed hunts, and total surprise attacks which accounted for 17.6% of attempts (Leonardi 1999). Although a degree of surprise is one of the most important factors in improving the hunting success in raptor species, Lanner falcons used this technique in only nine out of fifty-two observed attempts. Open attacks also allow time for anti-predatory behaviour in prey, which also reduces success rates (Leonardi 1999, 2002). Nevertheless, partial surprise was used significantly more often and pairs captured more prey than they did by using non-surprise attacks (Leonardi 1999). Interestingly, the use of cooperative hunting techniques were not uniformly distributed among prey flock classes. In fact, hunting success in relation to prey flock size was significant for partial surprise attacks on larger groups (22%) and non-surprise attacks on medium flocks (27%; Leonardi 1999).

Many examples of successful kills using cooperative hunting have been recorded. In one instance a pair was seen to hunt cooperatively and catch Red Bishops *Euplectes orix* from the flocks that they herded and hunted together (Kemp 1993). Larks were successfully captured by cooperative hunting in Layounne, Morocco (Bergier *et al.* 2013). At Niamey, Niger, two pairs of the local *F. b. abyssinicus* regularly hunt in pairs over flocks of Garganeys *Anas querquedula* and Ruffs *Philomachus pugnax* which rest or feed on the flooded banks of the River Niger (Giraudoux *et al.* 1988). A pair of Lanner falcons was observed predating feral pigeons in harvested wheat fields, with the male knocking the pigeon out of the sky and the female grabbing it on the ground (A. M. Muller pers. comm.). Partridges are known to be hunted cooperatively by Lanner falcons in Natal in South Africa, and Pigeons in Bulawayo in Zimbabwe (Gurney 1862, Francis 2013).

Adult Lanner falcons may also use cooperative hunting to teach their young different hunting techniques (Yosef 1991). Female *F. b. biarmicus* will often accompany the male on hunts once the chicks were older than two weeks (Stephenson 2001). Both members of a pair were seen to hunt together again after their young had fledged, when parents were also observed teaching their young how to hunting cooperatively by incorporating them in their foraging expeditions (Yosef 1991). They were extremely successful in catching pigeons, with the female stooping first at the pigeon and the male following higher overhead, the female mostly catching the prey after it had been struck by the male (Stephenson 2001). In this way, *F. b. tanypterus* females had significantly greater hunting success than males when hunting cooperatively with young (Yosef 1991).

Ground feeding

Prey captured on the ground by Lanner falcons mainly consists of invertebrates, small mammals, and lizards. Lanner falcons have been observed feeding on swarming locusts on the ground in Gargano, Apulia (Caldarella *et al.* 2005). Birds have also been known to snatch snakes and chameleons from the ground on the roads in Cape Province of South Africa (Pitman 1967).

Necrophagy

The remains of cats and Pine Marten *Martes martes* have been found in the diet of *F. b. feldeggii*, probably as a result of the birds feeding on carrion (Siracusa *et al.* 1988, Ciaccio *et al.* 1989). An adult Lanner falcon has been observed on a small farm road sitting on a freshly-killed Yellowbilled hornbill. The falcon attempted to fly off with the prey but was unable to carry the carcass (A. M. Muller pers. comm.).

In the Eastern Desert, Lanner falcons have been known to prey directly on large birds such as Crane, Common Buzzard, and White Stork that have become grounded due to exhaustion, or to feed on the carrion of birds that are already dead (Goodman and Haynes 1992). Sometimes remains of prey are found near to the nest of Lanner falcons but are not eaten. Remains of species such as Hamerkop *Scopus umbretta*, Cattle Egret *Bubulcus ibis*, and Black-shouldered Kite *Elanus caeruleus* have been found in these circumstances (Stephenson 2001). Stephenson (2001) also reported that the Hamerkop in this case was struck down below the nest by a female Lanner falcon, and the Black-shouldered Kite was killed after it harassed a recently fledged *juvenile*.

An adult male *F. b. biarmicus* was once been seen carrying the rib bone of an ostrich *Struthio camelus* that it had retrieved from an ostrich abattoir (Stephenson 2001) and *juvenile* Lanner falcons have been seen feeding on the remains of dead lambs in the company of Ravens (Stephenson 2001).

Kleptoparasitism

'*Piracy*' is one of the opportunistic techniques used by the Lanner falcon and its use is detailed in a number of published reports. A grounded Black-shouldered Kite has been recorded as a victim of piracy, being robbed of a small mammal by a Lanner falcon after an evasive flight (Reynolds 1974). A *juvenile* Lanner falcon was seen pirating a small prey item from an adult female Peregrine above the main street of a small town in South Africa (A. M. Muller pers. comm.). The Lanner falcon came from behind at high speed, turned over, and snatched the prey item from the talons of the Peregrine. The item was then eaten on the wing by the Lanner falcon (A. M. Muller pers. comm.).

In Socna, at Fezzan in Libya, a pair of Lanner falcons attacked a male Pallid Harrier *Circus macrourus* when it was hunting (Erard 1970). While the female chased it at the same level, the male swooped down on it almost vertically (Erard 1970). Another unidentified bird stole prey in mid-air from a Pallid Harrier in Khartoum, Sudan (Butler 1905). A Lanner falcon has also been recorded attacking a young African Hawk Eagle *Aquila spilogaster* in order to rob it of its prey.

A Yellow wagtail *Motacilla flava* was stolen from a Brown-necked Raven *Corvus ruficollis* that was forced to drop the prey so that it could be grabbed in mid-air by a Lanner falcon (Erard 1970). Afterwards, a group of Ravens attacked the Lanner and forced it to leave the prey but it soon managed to recover its meal (Erard 1970).

Two records of kleptoparasitism exist for *F. b. feldeggii* in Sicily, one case which intra-specific and the other of a Lanner falcon robbing a Lesser kestrel (Mebs 1959, Massa *et al.* 1991).

On the other hand, other predators have been known to steal prey from the Lanner falcon after a successful hunt. At the Polentswa water hole in Kgalagadi Transfronier Park, a Yellow-billed Kite *Milvus aegyptius* tried unsuccessfully to steal a Cape turtle dove *Streptopelia capicola* which had been caught by a Lanner falcon. In another instance, the large size of a Tawny eagle meant that it was able to steal prey from a Lanner falcon. Engel (2011) hypothesized that the Lanner falcon had successfully killed a Pygmy falcon *Polihierax semitorquatus*, and that it was subsequently robbed by a Tawny Eagle. In the same Park, a Black-backed jackal pirated a Lanner falcon that had caught a Cape Turtle dove. When the hunting Lanner falcon was successful, the Jackal came from about 400 metres away, and the Lanner falcon attempted to fly off with the dove. However, the slight uphill slope of the pan edge meant that the Lanner falcon struggled to lift the dove, so it was dropped and the jackal instantly collected it (A. M. Muller pers. comm.).

Bat hunting

Falcons have been observed hunting bats over drinking sites at dusk (Yosef, 1991). Bats emerged 15–30 minutes after sunset in darkness beyond the limits of human night-time vision and the Lanner falcons started hunting them after 15 minutes (Nichols and Campbell 1978, Thomsett 1987). In Kenya, *F. b. abyssinicus* frequently cached bats that it had caught and immediately resumed hunting them (Thomsett 1987). After falcons returned to their roosts they frequently ate the prey they had cached earlier (Thomsett 1987). No hunting of bats has been observed during the breeding season and no bats are known to have been used for feeding chicks. (Thomsett 1987). However, although *F. b. tanypterus* has been observed consuming bats at a perching site, some are certainly taken back to the nesting cliff (Yosef 1991). Urban-dwelling *F. b. biarmicus* are known to chase and eat bats in flight (Nichols and Campbell 1978). The wings are always removed prior to ingestion (Yosef 1991). In Durban in South Africa, Lanner falcons did not stoop but flew along in rapid but level flight, darting at bats as they passed, and capturing prey with a success rate of 10–12% (Nichols and Campbell 1978). A male *F. b. tanypterus* reportedly chased bats from above and behind with a success rate of 29% (Yosef 1991). Male and female *F. b. abyssinicus* hunt bats together, and their flights are often accompanied by repeated '*chup chup*' calls which are no doubt useful for communicating after complete darkness has fallen (Thomsett 1987). Cooperative hunts are more successful than birds hunting alone, and this technique is probably more useful for pair bonding and maintenance of nest sites than for simple food gain (Thomsett 1987).

Insect hunting

The Lanner falcon uses a technique similar to that performed by Eleonora's falcon, and uses slow wing beats to hover and grab insects such as flying ants (*Hymenopterae* and *Formicidae*) or termites in flight (Figure s.40; Massa *et al.* 1991).

7.9 Differences with the Peregrine

Morphologically, *F. b. minor* and *F. b. biarmicus* are very similar (Jenkins 1995). Overall, the flight mode of Peregrine falcons is energetically expensive due to the relatively small flight surfaces and the larger feet that are used to facilitate the capture of aerial prey (Jenkins 1995). In fact, Peregrine falcons show a greater preference than Lanner falcons for hunting from perches and to actively target flying prey (Jenkins 1995). Despite these structural similarities, the dietary overlap between sympatric Peregrine and Lanner falcons in South Africa was low (Jenkins and Avery 1999). Peregrine falcons often occupy a broader food niche than Lanner falcons but the latter consistently take a higher proportion of largely terrestrial and non-avian prey (Jenkins and Hockey 2001). Such differences lead to more active foraging by Lanner falcons, such as hunting on the ground, when compared to Peregrine falcons which are more specialized towards hunting active aerial prey (Jenkins and Hockey 2001). Jenkins and Hockey (2001) conclude that the success rate of hunts by Peregrine falcons is dependent on the abundance of the avian prey base and the effects of topography on foraging conditions (Jenkins and Hockey 2001). Latitudinal trends in prey availability, where resource availability decreases towards the Equator, tend to negatively influence Peregrine falcon abundance while leading to expanded Lanner falcon populations (Jenkins and Hockey 2001).

7.10 Defensive behaviour of prey

Several different defensive strategies are adopted by prey against Lanner falcon attacks. For example, Crowned Guinea Fowl *Numida meleagris* responded to repeated stoops by a Lanner falcon by the adults clustering closely around the chicks (Skead 1962). Once the Lanner falcon had landed on the ground, the Crowned Guinea Fowl ran towards it and attacked (Skead 1962). In Nigeria, Brandt (2006) observed defensive behaviours in feeding small passerines when *F. b. abyssinicus* approached to within one hundred metres. Lavender Waxbill *Estrilda caerulescens*, Black-rumped Waxbill *E. troglodytes*, Bronze Mannikin *Lonchura cucullata*, and Rock Firefinch *Lagonosticta sanguinodorsalis* all managed to take flight and escape, as did the more frequent Red-billed Firefinch *L. senegala* (Brandt 2006). Cinnamon-breasted Rock-bunting *Emberiza tahapisi* preferred to remain in alarm on the feeding patch when the other bird species flew away (Brandt 2006). The Blacksmith Plover *Vanellus armatus* has been observed giving an aposematic display in which the bird reacted to a fast low approach by a Lanner falcon by facing it with its wings partly spread and calling loudly (Thomas 1983). The suggestion was that this plover was distasteful (Thomas 1983).

In Sicily, colonies of Jackdaws and Rock pigeons regularly nest on the same cliffs as Lanner falcons (Ciaccio *et al.* 1989, Leonardi 1991). Nevertheless, the percentages of these species captured by cooperative hunting was lower (31%) than that observed in other Lanner falcon subspecies (50%; Yosef 1991, Kemp 1993). This low percentage may have been due to the anti-predator behaviour of the Jackdaws (Leonardi 1999, 2002). Large flocks of Jackdaws frequently use mobbing (43%) against Lanner falcons (Leonardi 2002). This active defence, combined with the dilution effect of the number of individuals in a flock, can improve survival rates in prey species (Leonardi 2001). It seems that the anti-predator reaction of the Jackdaws can be stimulated by the presence of single attacking individual, and they were particularly active in mobbing female Lanner falcons (Leonardi 2001). The differentiation between sexes, through the recognition of size differences for example, may therefore play a fundamental role in the choice of the correct response to a predator (Leonardi 2002). The significant result between the use of mobbing against non-surprise and partial-surprise attacks shows the important role of visual detection during surprise attacks (see *Cooperative hunting*; Leonardi 1999, 2002). The escape tactic appears to be the most effective response to unexpected attacks due to constant vigilance around the nesting cliff (Leonardi 2002).

Chapter 8.
Movements

8.1 Overview

The Lanner falcon is not a truly migratory species but may undertake local movements, possibly connected with weather conditions or food supply. It regularly migrates in response to seasonal rains and is also an altitudinal migrant in which at least some populations are known to migrate from high-altitude breeding areas to lower elevations during the non-breeding season. The main movements of the species are intra-African and are compatible with a possible colonization process especially along the borders of the Sahara desert (Figure 8.2).

Certain races such as *F. b. erlangeri* which are involved in long seasonal migratory movements are characterized by some slight flight specializations which mark them out from the more sedentary races. The nominate subspecies shows a tendency towards seasonal movements and also long journeys towards south-western and eastern Africa which seems to conform to the hypothesis that the species originated in southern Africa (Figures 8.2 and s24).

Figure 8.1 A *F. b. feldeggii* chick ringed with a coloured ring and alphanumeric code during research project in Eastern Sicily, Italy. © and courtesy of Giuseppina Dipasquale.

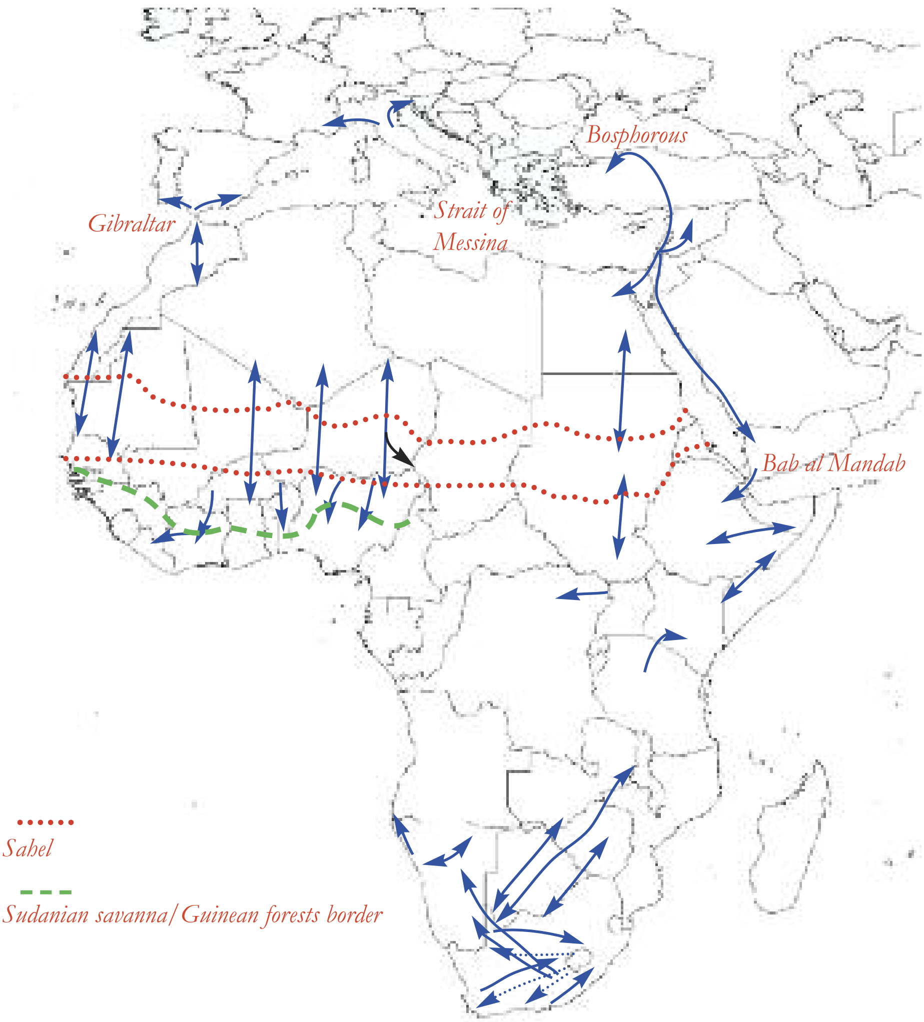


FIGURE 8.2 The principal medium and long-distance movements of the Lanner falcon races inside the known distributional area. The four main bottlenecks where Lanner falcons occurred are also shown. Particularly remarkable are the long distance movements made by migrant Lanner falcons from central and southern areas towards the Kalahari basin (Jensen 1972, Elgood *et al.* 1973, Smeenk 1974, Thiollay 1977, Curry-Lindahl 1981, Nikolaus 1987, Liversidge 1989, Van Zyl *et al.* 1994, Herremans and Herremans-Tonnoeyr 1996, Gatter 1997, Ash and Miskell 1998, Oatley *et al.* 1998, Shirihai *et al.* 2000, Hatzofe 2001, Thiollay 2006, Jensen *et al.* 2008, Dowsett-Lemaire and Dowsett 2014).

8.2 Intra-Palaearctic movements

In the Palearctic ecozone at least three subspecies (*F. b. biarmicus*, *F. b. erlangeri* and *F. b. tanypterus*) are associated with migratory movements. *F. b. feldeggii* seems, however, to be mainly sedentary and only undertakes short and local movements.

Falco biarmicus feldeggii

Data on movements of this race are scarce but observations that have been made seem to mainly have involved wandering *juvenile* birds and very few individuals have been observed along the main Palearctic migration routes. For example, a group of between 1 and 5 individuals was seen at the Bosphorous in Turkey during September. Between 1996 and 2000, there were a total of 8 individual sightings (1997 – 4, 1998 – 2, 1999 – 1, 2000 – 1) where birds were observed along the Messina Strait (Corso 2001). A sole individual was recorded along the eastern Black Sea flyway route in the locality of Agurkarkhana in the Kobuleti Lowland region of Ajaria, in south-western Georgia (Abuladze 2013). Scattered records have been gathered from many countries up until 1999: France has 22 records, the Czech Republic 1 or 2, Romania has 3+, and there are 3 from Malta (Corso 2000).

More data are available on wintering birds and *juvenile* birds dispersing after the breeding season. The Lanner falcon has been regularly recorded wintering in the Camargue region of France, with eleven sightings (2001–2006) mainly of immature birds but also notably adults of both *F. b. feldeggii* and *F. b. erlangeri* (Kayser *et al.* 2008). In Tuscany, many wintering birds (also *juveniles*) have been observed in coastal areas such as Maremma, and less frequently in central areas and on the northern coasts. The Lanner falcon seems to be an irregular migratory visitor wintering in the Circeo National Park (Central Italy) and at San Bartolo (Marches) with 0–1 individuals in nine years (1998–2005). During 1990–1997 in Sicily, Corso and Iapichino (1998) observed more than 180 individuals, mainly immature birds plus some adults, wintering in low altitude areas (at around 100–700 metres above sea level; minimum 0, maximum 1280 metres). A few immature birds have also been seen in the Peloritani Mountains in northern Sicily during February and March. Due to the large number of immature birds captured (around 400 in total, with a maximum of 43 in one year) in Apulia, Orlando (1957) hypothesized that this may have been due to an influx of migrants, mainly from the Balkans. Valentini (1957) also proposed a regular passage across the sea in October and November, together with migratory finches and larks. He regularly observed and captured Lanner falcons, especially during the onset of the migration of small passerines (Valentini 1957). It is probable that these Lanner falcon individuals, mainly *juveniles*, exploited this abundant and readily available food source as their African counterparts do, by aggregating along the main migration routes (Massa *et al.* 1991).

The *F. b. feldeggii* race is widespread throughout Turkey but is relatively uncommon on passage, principally during the autumn, between mid-September and mid-October, and in winter where it can frequently be found in coastal areas and wetlands (Kirwan *et al.* 2008). Nevertheless, recent data on tracked *F. b. tanypterus* from Israel demonstrate a possible route from the Middle East to central and northern Turkey

(Hatzofe 2001). Further research is also required for the small breeding population at Lake Urmia where *F. b. feldeggii* is presumably a summer visitor during the month of August (Scott 2008).

Falco biarmicus tanypterus

The seasonal movements of this race are well known but it remains unclear exactly how many individuals are involved during passages. Very small numbers of migrants appear to cross Israel and the Sinai peninsula towards the Gulf of Suez and birds have been observed in Yemen, the Arabian peninsula, and Iraq with some movements into the interior of the Jordanian desert, perhaps due to some wandering birds, whilst there have been only a very few records from Cyprus (Shirihai *et al.* 2000). In common with other subspecies, *F. b. tanypterus* favours upland areas for breeding but can also be found in more open and low-lying regions (Shirihai *et al.* 2000). Only two individuals have been recorded at Zait Bay in Egypt, situated in the middle of the West Asian–East African migratory flyway which is used by very large numbers of soaring migrants. Despite the relatively small numbers of observations of passing individuals, hundreds of Lanner falcons are captured annually in bottlenecks such as Bab al Mandab and along the Red Sea (see Chapter 9). In addition, as is often the case with the African races, there are often large aggregations of individuals. For example, in one case twenty-one were observed together, with at least five immature birds, resting on telegraph poles along 130 kilometres of desert road between pumping stations in Syria (Leonardi *et al.* 1992).

Autumn passage occurs from the middle of September through to late November with a peak between mid-September and mid-October (Shirihai *et al.* 2000). The total numbers observed in Israel each year ranged from 20 to 30, recorded either in small groups of around 2–3 individuals, or as solitary birds (Meinertzhagen 1920, Shirihai *et al.* 2000). In fact, in the northern valleys of Israel, it seems that only relatively small numbers of migrants or winter immigrants occur (based on records from 1990–1999). It is a rare winter visitor, and is occasionally seen in the northern Negev. One was seen in October 1980 near Suez in Egypt. It has also been observed near Jaffa and in the Shfela region of Israel in late December (Meinertzhagen 1920). The Lanner falcon is a scarce winter visitor in the Riyadh region of Saudi Arabia, and has been recorded occasionally between October and February (Stagg 1987). In Sudan, it is a Palearctic migrant with observations occurring mainly between October and February (Nikolaus 1987). At Zaranik in the Sinai region of Egypt, it is observed as an occasional passage migrant in October. Nine individuals crossed into Djibouti in the autumn of 1987 (Shirihai *et al.* 2000). Five Lanner falcons were seen together at Sana'a in Yemen, on 3rd September 1979 (Leonardi *et al.* 1992) and it has also been observed during autumn passage at Al Khirba es Samra in Jordan.

Spring passage is less significant than in autumn and occurs from mid-February to mid-May with a peak in the second half of March (Shirihai *et al.* 2000). Most occur in the south and east with a maximum of seven individuals (mainly immature birds) seen in Elat between 1977–1988 (Christensen *et al.* 1982, Yosef 1995, Shirihai *et al.* 2000). Two individuals were seen near Suez on the 28 February and again on the 10 March, and several Lanner falcons were reported in Lahmi and Hamata (Red Sea, Egypt) in April and May (M. Habib pers. comm.). Five individuals were seen in March and April at Gebel el Zeit in Egypt and the species was found near water in the St. Katherine monastery area of Egypt in May and June, and in the Beqaa region of Lebanon, over mountains, coasts, and islands in August and early May (Meakin *et al* 2005, Ramadan-Jaradi *et al.* 2008).

A specimen of *F. b. tanypterus* was collected at Al-Faw in Iraq on 30 August 1886 (Leonardi *et al.* 1992). Small numbers have been observed passing through Cyprus between September–November and February–April (Shirihai *et al.* 2000). In the southern Arabian peninsula it is recorded singly from July to February (except in Bahrain), and there has been only one record from Qatar. In North Yemen it has been recorded as present in winter, although only rarely, in spring, and, most commonly, in autumn. In spring, both races (*F. b. tanypterus* and *F. b. abyssinicus*) are present. It would seem to be a passage migrant and winter visitor in small numbers, but also an uncommon breeding resident (Brooks *et al.* 1987). At the Ras Siyyan–Bab el Manded strait in Djibouti, two individuals were seen in the first week of March.

Dispersal routes taken by individual *juveniles* after release show dispersion patterns toward both the north and south (Hatzofe 2001). Tracked individuals reach northern and south-eastern Turkey, others remained in Israel (Western Galilee and Western Negev), and one individual was captured in south-western Saudi Arabia (Figure 8.2; Hatzofe 2001). Outside its distribution range, a *F. b. tanypterus* has been found to reach as far afield as Togo (Mango and Kourniere), Eritrea, and northern Ethiopia (Leonardi *et al.* 1992, Cheke and Walsh 1996).

Falco biarmicus erlangeri

Jany (1960) proposed a seasonal movement of breeding pairs of *F. b. erlangeri* towards desert areas where they reared young in a short time window which coincided with the passage of migrant passerine species. It is not therefore a truly migratory species but some individual birds may wander or move seasonally, and in southern Algeria the species can reach as far south as the Sahara (Ledant *et al.* 1981).

Wandering *juvenile* Lanner falcons have been known to reach the Iberian peninsula and observations have been made in Portugal, Spain, and Gibraltar (Figure 8.2: Corso 2000). Around twenty sightings have been recorded from the European coast of the Gibraltar straits ranging between February and September (Daly 2008).

Interestingly, *juveniles* were observed mainly in June and September and immature birds in April (Daly 2008).

Mauritania represents the southern border of the distribution of this race and also a contact zone with *F. b. abyssinicus*. *F. b. erlangeri*, all of which have been observed near Akjoujkt, Tichitt, Tidjikja in August, and between October and December (Gee 1984). Birds have also been seen in the eastern area of Nouakchott in August, April, October, and November (Gee 1984, P.W.P. Browne pers. comm.). One adult *F. b. erlangeri* was seen at Chott Bull just north of Parc National du Diawling near the border with Senegal (P.W.P. Browne pers. comm.). The race also occasionally migrates into Senegal, although it seems to limited to a winter visitor in the northern part of this country (Curry-Lindahl 1981, Schifter von 1986). One individual was collected on the 5th January near Richiard Toll Station, and it has been observed on at least three other occasions in the same area. In Mali, *F. b. erlangeri* is a Palearctic migrant with sightings beginning in April and numbers have usually peaking in August (Lamarche 1980).

Regular movements occur in winter in Morocco (Tangier area, Gibraltar, and Tafilalet) and Algeria where *F. b. erlangeri* can be seen moving towards wetlands and wadi estuaries where it exploits the large number of shorebirds (Bergier 1987, Isenmann and Moali 2000). In eastern Morocco, Lanner falcons occupy Mediterranean cultivated areas at high densities between November and February, with numbers at least 5–6 times greater than during the breeding season (Bergier 1987).

There have been no observations or captures of *F. b. erlangeri* in Sicily (Orlando 1957).

8.3 Afro-tropical movements

Both of the Afro-tropical subspecies of Lanner falcon (*F. b. abyssinicus* and *F. b. biarmicus*) make medium and long-distance movements in relation to periodical rains and following the movements of prey sources which makes them facultative migrant species (Zyl, van *et al.* 1994). This tendency is also confirmed by the very long distances travelled such as a *F. b. biarmicus* individual that made a direct flight of 450 kilometres or the flights recorded from North Cape to Malawi, which lies at a distance of around 2,090 kilometres to the north-east (MacLean 1984, Little 1991).

Falco biarmicus abyssinicus

Movements of this race can be separated geographically into eastern and western. In eastern Africa, several observations have been made regarding birds that cross the Bab al Mandab bottleneck (Figure 8.2). Across this strait, the Lanner falcon is a presumed occasional migrant with less than ten individuals passing by each year

(Welch and Welch 1988). Scattered data confirm the low number of birds: only 1–2 birds on four days between 9–31 October 1987 at Doumeira, 8 individuals recorded from 15 October to 3 November, and around 1–4 birds over Djbouti in midwinter (Ash and Atkins 2009). Nikolaus (1987) considered *F. b. abyssinicus* as an at least partially migratory species, which was present in South Sudan, but not as a breeding species (Figure 8.2). In Somalia, Lanner falcons arrive in cold weather from October to January, possibly from the Ethiopian highlands, and leave again about March (Ash and Miskell 1998).

In west Africa the Lanner falcon is locally migratory, moving south into the moister Guinean savannas during the dry season where it probably breeds, and then moving north towards the Sahel during the wet season (Figure 8.2; Thiollay 1978, Brown *et al.* 1982). In fact, it is usually absent from the Guinean savannah belt between July–October, with a corresponding influx into the Sahelian belt usually observed during the same period. An increase in the number of Lanner falcons present in Nigeria takes place between December–May when it is breeding (with passage at Zaria in May), and in Somalia between October–March. In the north-western regions of the Democratic Republic of Congo, the species is present in December–March when it is non-breeding (Curry-Lindahl 1981). The northern distributional limit is at 8°N in Nigeria where it is regularly present in October–June occupying broadleaved savannas and forest mosaics (Brown *et al.* 1982). Stragglers are present up until July and it is absent only between August–September (Brown *et al.* 1982). In fact, as observed by Elgood (1982), Lanner falcons are observed mostly in the dry season in the south but more records occur during the rains in the extreme north, which indicates some seasonal movements. Numbers in Nigeria may therefore be due to an increase during the dry season possibly derived from the north where no diminution in numbers occurs during any season (Elgood *et al.* 1973, Thiollay 1977). The species is therefore widespread throughout Nigeria during the dry season, although it mainly avoids the rains in the central and southern regions between August–September (Elgood *et al.* 1973).

It is also abundant during the dry season in the Ivory Coast, in Yankari National Park in north-eastern Nigeria, in Falgore (Kogin Kano) Game Reserve, usually in January and between March–May, and also in the Kagoro Hills (Nindam Forest Reserve). It is uncommon in aggregated groups in northern Liberia during January, February, and April (Dyer *et al.* 1986, Gatter 1997). In Ghana, fewer records occur during the peak of the rains and sightings of Lanner falcons are uncommon in the dry season, although some have been seen in August–October at all latitudes (Cheke and Walsh 1996, Dowsett-Lemaire and Dowsett 2014). It is regularly sighted at the Cape Coast in Ghana at the edges of pans, lagoons, and beaches, and one individual has even been reported at sea off Accra, alighting on a ship (Dowsett-Lemaire and Dowsett 2014). Some individuals can reach the coastal savannas of Benin between

October–May, whereas *F. b. abyssinicus* can be found in Senegal all year round (Thiollay 1977).

During the dry season there is an abundance of raptors in southern Burkina Faso, and Lanner falcons remained at least as abundant over a number of years as can be seen when figures from 1972, when 3 individuals were recorded, are compared with those of 2002, when 6 individuals were recorded in woodlands and 5 in cultivated areas (Thiollay 2006). A quantitative analysis made by Thiollay (1977), revealed a density of 0.1–0.2 individuals/kilometre in the Guinean Zone during the dry season (it was absent from July to October), and 0.5–1 individuals/kilometre in the Sudanian Zone. Presence was continuous all year round in the north and was reduced by a half during the rainy season in the south (Figure 8.3). Instead, raptor diversity was highest in the dense, relatively well-preserved Guinea savannas, and raptor species richness was higher there than in the Sudan zone, largely reflecting patterns of community richness and diversity in the Afro-tropical raptor assemblage (Buij *et al.* 2013).

In the Sahelian zone there is small resident populations (0.7 individuals/100 kilometres) except the central delta and flood plain when it rains where the density is 3 individuals/100 kilometres from July to October (Figure 8.3; Thiollay 1977). It is capable of reaching as far as Adrar des Ifoghas, a massif in Mali's Kidal Region that extends into Algeria, and Tanezrouft in southern Algeria, with densities increasing from 0.2–0.4 individuals/100 kilometres during March to early August, increasing to 3–8 individuals/100 kilometres between late August and mid-September (Thiollay 1977). Similar densities are found in south-eastern Niger, where up to 1.4–1.7 individuals per km^2 are found in August–October, particularly in areas with feeding flocks of Abdim's Stork *Ciconia abdimii* which feed on grasshoppers (Jensen *et al.* 2008). It seems likely that several hundred Lanner falcons were congregated in south-eastern Niger during these periods (Jensen *et al.* 2008). In the former Northern Gobir region of Niger, the Lanner falcon avoids the hot season but they are known to follow some seasonal movements during the rains through to harvest time, and during the cold seasons (Manvell 2010).

Falco biarmicus biarmicus

This race is a partial migrant in southern Africa with birds (most often *juveniles*) which breed on the eastern escarpment of South Africa moving in to the dry western regions of South Africa (Zyl, van *et al.* 1994, Jenkins 1995, Parker 1999). This east-west axis of movement partially mirrors the annual movements of Namaqua sandgrouse *Pterocles namaqua* in the western half the country (Zyl, van *et al.* 1994). Lanner falcons apparently move into flat, open areas without cliffs during the summer (Jenkins 1994). In arid areas (such as the Kalahari, Karoo, and Namib), they are often

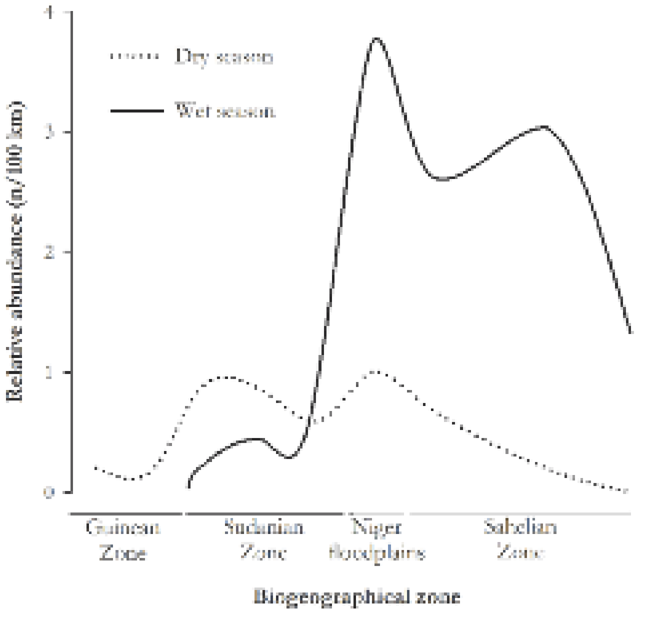


FIGURE 8.3 Relative densities of *F. b. abyssinicus* in different biogeographic zones of West Africa during both dry and wet seasons (Thiollay 1977).

nomadic, appearing locally in numbers for short periods, perhaps in response to rainfall, and then moving away again (Brown *et al.* 1982). Such nomadic individuals may not be territorial breeding birds, but surplus adults, sub-adults, and *juveniles* (A. C. Kemp quoted in Brown *et al.* 1982). In the Karibib district of central Namibia the pattern of movement presumably follows the pattern of local rains and the resultant local abundance of Harvester termite *Hodotermes mossambicus* flights, and a local aggregation of 15 *juveniles* and 5 adults was seen on 19th January for example (Jensen 1972). The Lanner falcon is often gregarious, and has been observed in flocks of twenty or more birds around waterholes (MacLean 1984).

In Botswana during the wet season, immature birds outnumbered adults by a factor of 1.6:1 (Herremans and Herremans-Tonnoeyr 1996). Local influxes may occur, especially when termites are swarming or large flocks of Red-billed Quelea *Quelea quelea* and quails are present, mainly around November–March (Finch-Davies 1920, Lack *et al.* 1980). The significant increases in the number of Lanner falcons reported in the Nama Karoo and in the southern Kalahari during the non-breeding season were not matched by equivalent decreases in numbers reported in other areas of South Africa, and so may be indicative of migratory influxes from the north (Figure 8.2; Jenkins 1994). In Zimbabwe, post-breeding dispersal movements occur in the south-western region during the rains, but seem to depend to some extent on their intensity (Irwin 1981). In the Dar es Salaam area of Tanzania, the Lanner falcon is seen only during March and April in areas of mangroves, coastal scrub, and salt pans (Harvey and Howell 1987). There are too few observations in central Mozambique for any pattern of seasonal movements to be apparent (Parker 1999). In Botswana, movements occur in small groups of immature birds (3–10 individuals) seen flying together in several of the northern areas between February and April (Penry 1994). In the same country, Lanner falcons were observed about five times more frequently during the wet summer months of October–February than during the dry winter months of June-September (Herremans and Herremans-Tonnoeyr 1996).

In the Kgalagadi Transfrontier Park in South Africa, the Lanner falcon is a migrant species with a late summer influx affected by rainfall, and it may well also be attracted by the high availability of prey in the form of swarming termites (Liversidge 1989). From a long-term study in the former Kalahari National Park, the peak abundances follow a similar pattern to that observed in the eastern African populations (Figure 8.4; immature/adult ratio = 2.5:1; Liversidge 1989, Zyl, van *et al.* 1994). In fact, similar concentrations of Lanner falcons during the same months have been recorded in the arid Tsavo East National Park in Kenya, between November and March (during the wet season), usually concentrated around water-holes where they hunt among huge flocks of *Quelea quelea* and swarms of termites (Figure 8.4; Smeenk 1974, Britton 1980, Lewis and Pomeroy 1989). The same pattern occurs in Botswana (based on records from 1992–1995), with a definite peak in the middle of the wet season (January), while numbers dropped drastically in late summer (March), and were low in autumn (April–May; Figure 8.5; Herremans and Herremans-Tonnoeyr 1996). Nevertheless, the peak abundance in Botswana (in the centre of the Kalahari basin) starts about two months earlier than in South Africa, and ends earlier than in the Cape Province (Zyl, van *et al.* 1994, Herremans and Herremans-Tonnoeyr 1996).

A detailed study was made on the seasonal movements of *F. b. biarmicus* in South Africa (Zyl, van *et al.* 1994). Confirming the conclusions drawn from previous studies, the numbers of Lanner falcons found in the Bushmanland area peaked in January, and in the Kalahari during March, with similar patterns for the Western Cape Province (Zyl, van *et al.* 1994).

No significant differences were observed between the Little Karoo, the southern Orange Free State, the north-eastern Cape, and the western and northern regions of the former Transvaal (Zyl, van *et al.* 1994). Immature Lanner falcons outnumbered adults by as much as 4:1, a ratio that defines this falcon as a differential migrant species, although no differences occur in the movement patterns of male and female birds (Zyl, van *et al.* 1994). Interestingly, dispersal patterns (such as towards the south-western coastal plains of South Africa; Figure 8.2) may be facilitated by the recent establishment of cereal croplands in these areas that have in turn attracted

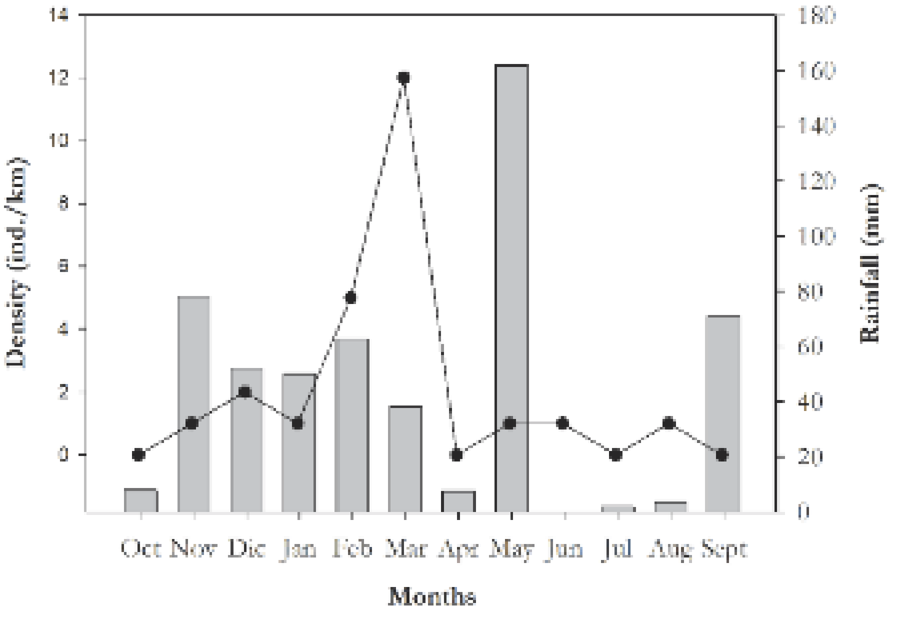


FIGURE 8.4 Relative densities of *F. b. biarmicus* in the former Kalahari National Park (1973–1983; Liversidge 1989).

large numbers of prey species such as granivorous birds and rodents (immature/adult ratio = 4.3:1; Zyl, van *et al.* 1994).

8.4 Ringed and tagged individuals

Oatley *et al.* (1998) reported 621 Lanner falcons ringed in the period 1948–1998 with 30 recoveries (4.6%). From an analysis of the ringing returns, there appears to be some long-distance dispersal in the central region of southern Africa, with one adult recovered 2,087 kilometres from the ringing site (Zyl, van *et al.* 1994). The same Author also notes that the Lanner falcon is not attracted to a Balchatri trap, though it can be caught efficiently in a dugaza net (Oatley *et al.* 1998). Two Lanner falcons ringed in central Namibia in December and January were recovered in February and October in the southern Orange Free State and the north-eastern Cape areas, over 1,000 kilometres to the southeast (Van Zyl *et al.* 1994). Nevertheless, of four Lanner falcon recoveries made in the former Transvaal state, and nine in Natal, none had travelled further than fifty kilometres from the ringing locality (Zyl, van *et al.* 1994). Movements appear to be much shorter along the South African coastal areas, with only one record of a *juvenile* that was ringed in the Western Cape and recovered 672 kilometres away in the Eastern Cape. Three chicks from nests in urban

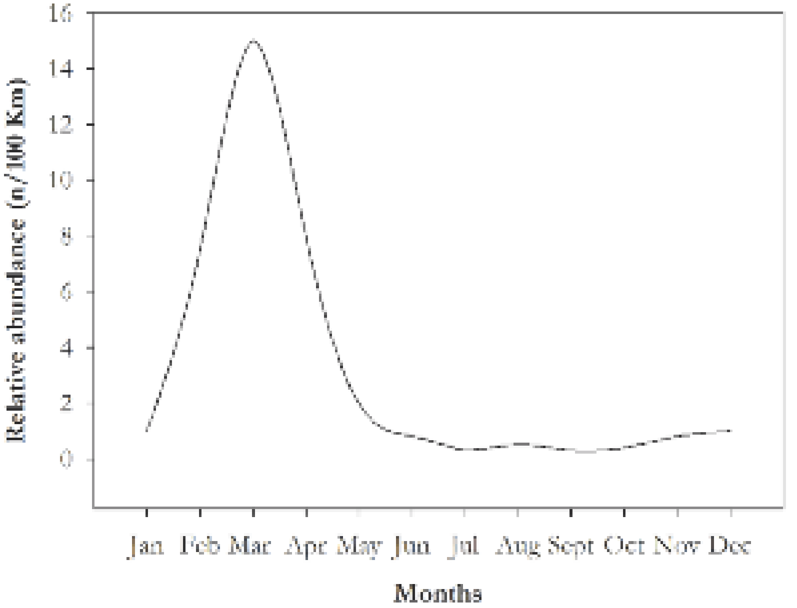


FIGURE 8.5 Relative densities of *F. b. biarmicus* in the former Tsavo East National Park in relation to levels of rainfall (Smeenk 1974).

sites in Harare were ringed in 1972 (Kellow-Webb and Dingley 1972). The only male of this brood flew from the nest early and it was recovered over seventeen years later only twenty-seven kilometres from where it was ringed (Mundy and Hartley 2002).

An adult female ringed in the outskirts of Harare was observed nesting in the city centre in subsequent years (Deacon *et al.* 2002). An adult Lanner falcon ringed on 7 March 1991 in the Kalahari National Park in South Africa was found dead on 9 June 1992 in the Choma district of Zambia, 1,200 kilometres to the northeast (Dowsett *et al.* 2008). Only one bird was ringed in Zambia between 2000–2005 (Roxburgh and Leonard 2007), and two adult Lanner falcons were captured in the forest fragments of the Taita Hills, south-eastern Kenya. Between 1960 and 1981 only five individuals were ringed in eastern Africa. A male was tagged with a patagial tag near Pretoria (Kemp 1993). In southern Africa, twenty-six free-flying Lanner falcons and fourteen nestlings were ringed between 1999–2000. Another study ringed ten birds in 2001–2002 (Oschadleus 2000, 2003).

Eighty-two Lanner falcon adults, both *juveniles* and chicks were colour ringed in the Eastern Cape (between 1992–2000) but there were only five recoveries (Stephenson 2001). No long-distance movement was reported, and the greatest distance between the ringing site and the subsequent recovery was 152 kilometres. In this case it was a female ringed as a ten-month old *juvenile* near its nest site which was recovered two years later mature and ready to breed (Stephenson 2001). Another bird was recaptured only 127 kilometres from the site where it was ringed. One adult male was recovered only 19 kilometres from the original nest site, fourteen months after being ringed (Stephenson 2001). A female was recovered (dead after having been electrocuted) at the same location where it was ringed almost three years earlier (Stephenson 2001). During a recent (2002–2005) study project in eastern Sicily sixty-two chicks were ringed with colour rings but there were no recoveries (Cipriano 2005, Leonardi *et al.* unpubl. data). A similar study in Calabria found that after three years effort of capture and ringing birds, no birds were recaptured or recovered in subsequent years (Mirabelli 1982). A male *F. b. tanypterus* was tagged in 1988 in the Negev Desert with a yellow ring on its left leg (Yosef 1988).

Chapter 9.
Threats and conservation

9.1 Introduction

The Lanner falcon has a very wide distribution range and there are a number of limiting factors which lead to differences in local abundance across the different parts of this range. This is especially evident when comparing the Palearctic and Afrotropical distributions of the species (Figure s31). Considering the African origin of the species and the role of the Sahara desert as a natural barrier, populations in the Mediterranean and Middle East become more vulnerable to limiting factors due to the structures of these metapopulations. Both intrinsic and external factors therefore combine to affect the survival of particular population demes (Andreotti *et al.* 2008). In this way, the Lanner falcon in Europe is considered to be a threatened species while in the Afrotropics it is the most widely-distributed, abundant, and competitive large falcon. In Ghana, for instance, conservation is of no concern and the Lanner falcon seems equally widespread today as it was in the 1930s (Dowsett-Lemaire and

Figure 9.1 A large group of *F. b. tanypterus* along with twelve Saker falcons, confiscated from a falconer in 2003. © and courtesy of Mohamed Habibi (Red Sea Protectorate).

Dowsett 2014). The main conservation challenge is therefore to ascertain the predominant local constraints and to evaluate their relative long-term effects.

Threats derived from human activities affect all races of the Lanner falcon and include direct persecution, nest robbery, drowning, electrocution, and collisions (Stephenson 2001). Other factors include the continuing loss of suitable habitats and the intensive use of pesticides in agriculture (Gustin *et al.* 2002, Andreotti and Leonardi 2007). Many additional threats occur during the post-fledging period when young are most vulnerable and it is possible that as few as two chicks out of five survive the fledging period (Kemp 1993). Mortality rates and their consequent effect on recruitment also have an important role to play in the maintenance of a viable population. Although the Lanner falcon can live for as many as eighteen or twenty years in captivity, the mean life expectancy of wild birds is usually around five years (Figure 9.2; Bree 1859, Kemp 1993), although there is a record of a ringed bird in Zimbabwe which was recovered after more than 17 years (Mundy and Hartley 2002).

Another problem resulting from the low detection rates for the species in the field is that the size of breeding populations can often be under-estimated, which may be the case, for example, in Turkey (Kirwan *et al.* 2008).

9.2 Human Disturbance

No quantitative data exist on the effects of human disturbance on the breeding success of the Lanner falcon. Several scattered and anecdotal reports give details that show a wide range of responses to human disturbance, from indifference to quite strong negative reactions (Andreotti and Leonardi 2007). Since the 1970s all species of large falcons at cliff sites in Kenya, including the Lanner falcon, have declined in numbers outside protected areas due to the effects of human disturbance (S. Thomsett pers. comm.). Even in areas of marginal human disturbance, such as livestock-rearing or communal land, the increase in numbers of Olive baboons *Papio anubis* to double or quadruple their previous numbers has had a very obvious impact on cliff nesting species (S. Thomsett pers. comm.).

Farms, villages, or small industrial sites located in the vicinity of breeding sites do not seem to have an apparent influence on productivity and occupancy (Andreotti and Leonardi 2007). Similarly the presence of asphalt roads close to nests seems to have a minimal impact (Andreotti and Leonardi 2007). More marked effects are evidently caused by recreational activities such as hiking, paragliding, climbing, and motocross, as well as birdwatching, photographic safaris, and other forms of nature tourism which are inadequately controlled (Andreotti and Leonardi 2007).

The Italian Action Plan for the Lanner falcon includes a protocol for research activities involving nest checking, chick handling, and sampling techniques with the aim of minimising disturbance (Leonardi *et al.* 2007). During a research project in

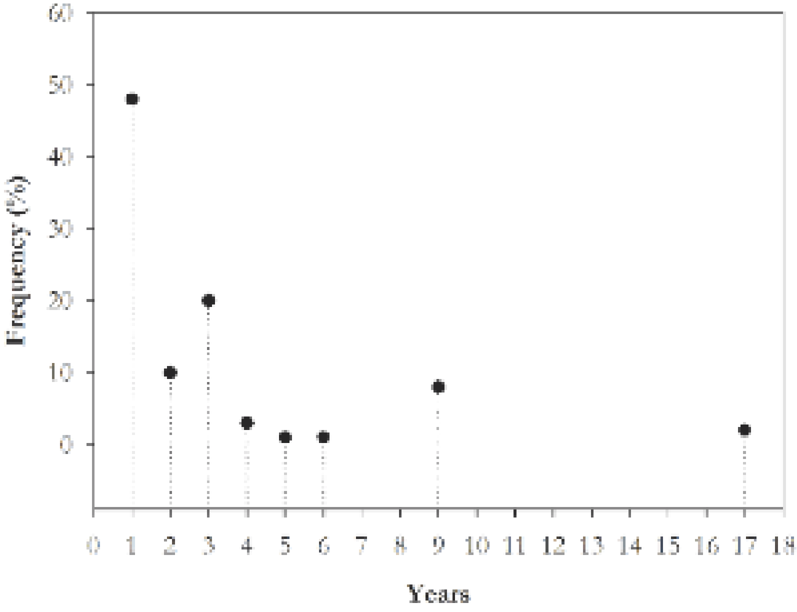


FIGURE 9.2 Frequency of the recovery of ringed Lanner falcons divided by the time elapsed since they were ringed (Oatley *et al.* 1998).

eastern Sicily between 2003–2006, more than fifty active nests were checked without any negative effects on productivity or on the survival of young birds (Amato *et al.* 2014). Interestingly, no aggressive reactions by parents were observed (Leonardi *et al.* unpl. data). In Harare in Zimbabwe, Lanner falcons were exposed to continuous human presence an the adjacent office (> 3 metres from the nest) during incubation for up to eights hour a day, five days a week, but no detrimental effects on productivity were observed (Deacon *et al.* 2002). The disturbance at this site even included a thirty-minute-long fireworks display around 200 metres from the nest site (Deacon *et al.* 2002).

9.3 Direct persecution

In common with other raptor species, *F. b. feldeggii* suffered a sharp decline in numbers during the 1950s and 1970s largely due to persecution and the trading of chicks and eggs for use in falconry (Andreotti and Leonardi 2007). It is difficult to quantify the direct effects of this pressure but the impact on the population has been considerable. For instance in Sicily in 1967 alone, twenty-three young Lanner falcons were taken from nests, while adults and young continued to be killed or captured up until the 1970s in Emilia-Romagna in Northern Italy (Bijleveld 1974, Chiavetta 1982).

In southern Africa, the Lanner Falcon frequently takes domestic chickens as prey (Barbour 1971), although this appears to happen on a very small scale, and on farms where domestic poultry *Gallus gallus* is not the dominant farming activity (Stephenson 2001). Nevertheless, it is possible that these farmers may retaliate by shooting the perceived culprits (Anderson 2000, Stephenson 2001).

Lanner falcons (particularly *F. b. biarmicus* and *F. b. abyssinicus*) have learned to use pylons and cell phone towers as nesting sites, but in Kenya such nests are destroyed as part of a national policy (S. Thomsett pers. comm.). In Ethiopia the tree-nesting *F. b. abyssinicus* has continued to flourish and, despite state-subsidised mass rodent poisoning on the Highlands, high densities of pairs remain nesting in mature eucalyptus trees (S. Thomsett).

In 1988 an individual was shot in Siena province in northern Italy, and another two immature birds were shot in Rimini Province and in Pianura Padana (Morimando *et al.* 1994). Another fourteen individuals were killed in Marches between 1981–1988, and five *juvenile* birds in Sicily between 1995–1998 (Ciaccio *et al.* 1989, Andreotti and Leonardi 2007). Ten individuals (50% *juveniles*) killed in Catania province (Eastern Sicily) between 1981-1984 (Ciaccio *et al.* 1989).

9.4 Predation

As a top predator, the Lanner falcon only rarely itself becomes prey. In Eastern Cape, Lanner falcons breed in inaccessible sites in order to avoid predators such as Baboons *Papio ursinus*, Velvet Monkeys *Cercopithecus pygerythrus*, and genets *Genetta* sp. (Stephenson 2001). Snelling (1973) reported a young male that was collected from a clutch of four chicks in a nest in Transvaal and eaten by a resident Bantu. One captive Lanner falcon has reportedly been killed by safari ants (*Dorylus* sp.) which are voracious carnivores and hunt in large numbers at night. In the wild they kill free-living birds at roosts near the ground (Cooper 1973). Another individual was found covered in ants but was able to regain 20% of its mobility after rehabilitation (Mundy and Hartley 2002). It seems that *F. b. erlangeri* could be preyed on by Pharaoh Eagle-Owl *Bubo ascalaphus* from the evidence of pellets and body remains recovered from Cap Tafarit, Parc National du Banc d'Arguin (Kayser 2012).

	1999	2000	2001	2002	2003	2004
Recovered	17	30	45	60	58	55
Deceased	2	4	2	4	2	3

Table 9.1 Numbers of captive Lanner falcons treated at the hospital of the Research Institute of the Fahad bin Sultan Falcon Center, Riyadh, in the Kingdom of Saudi Arabia. Mortality rates were 2.1% (n = 267; Samour and Naldo 2005).

9.5 Illness and mortality

Many causes of illness and mortality have been reported for the Lanner falcon (Table 9.1). Most of these reports are from captive birds so, unfortunately, the impact of these threats in the wild is unknown.

9.6 Infectious diseases

Parasitic diseases

Species of the genus *Caryospora* (apicomplexan protozoan parasites) appear to be the more pathogenic to raptors, particularly to young birds under captive conditions. Weight loss, reduced appetite, regurgitation and vomiting, blood in faeces, diarrhoea, and acute death characterize clinical coccidiosis. Similar clinical signs, together with poor performance during training exercises, have frequently been observed in captive falcons in the Middle East, particularly in *juvenile* Peregrine, Barbary, and Lanner falcons. *Haemoproteus tinnunculi* (*Protozoa, Apicomplexa*) is known to have infested *F. b. abyssinicus* in the Ethiopian region. In fact, gametocytes grow around the nucleus of infected erythrocytes (Valkiunas 2004). Examination of coccidian parasites from Lanner falcons revealed one previously unreported species of *Eimeria* from Saudi Arabia. A total of forty adult Lanner falcons were examined for coccidian infection. Two of them were infected (5%) with an entirely new species of *Eimeria*, so the specific name *biarmicus* was derived from the species name of the host. In summary two species were recognized: *E. falconensis* 27.2 × 18.1 (Oocysts, mean μm) 11 × 6.9 (Sporocysts, mean μm) and *E. biarmicus* sp. n. 22.4 × 17.9 (Oocysts, mean μm) 10.1 × 6.1 (Sporocysts, mean μm). Other Coccidia have been found infecting birds in Europe including *Caryospora kutzeri* 38.7 × 34.1 (Oocysts, μm) 24.6 × 21.0 (Sporocyst,s μm) and *Caryspora neofalconis* 27.0 × 23.8 (Oocysts, μm) 18.8 × 14.8 (Sporocysts, μm) (Boer 1982). Infected birds develop diarrhoea and become listless and anorexic (Boer 1982).

There is little evidence that helminths are primary pathogens, except for heavy infestation. Nevertheless, a Lanner falcon died due to a heavy infestation of the acanthocephalan *Polymorphus boschadis* (phylum *Acanthocephala*) (Keymer 1972). Infections with acanthocephalans are rare. These parasites are generally found in the distal small intestine with their proboscids firmly embedded in the mucosa (Keymer 1972).

One emaciated bird found in Zimbabwe had a severe infestation of tapeworms (*Cestoda*, phylum *Platyhelminthes*) and increased in weight by 18% after treatment (Mundy and Hartley 2002). Tapeworms (*Dispharynx* sp. *Nematoda*: *Acuariidae*) were also found in the stomach of a female Lanner falcon in South Africa (Bangs and

Loveridge 1933). Other parasites associated with Lanner falcons include *Matabelea fuhrmanni* (*Cestoda, Cyclophyllidea, Paruterinidae*) found in *F. b. biarmicus* in Unzanganzi, Zimbabwe (Baer 1933). Both *Serratospiculum chungi* (*Nematoda, Diplotriaenidae* family) (Gibson *et al.* 2005) and *Strigea falconis* (*Platyhelminthes*, *Trematoda*) have been found in the intestines of Lanner falcons (McDonald 1969). Adult *Physaloptera alata* (Nematodes, *Physalopteridae* family) worms have also been found attached to the oesophagus of a Lanner falcon, although this was an incidental finding during a routine endoscopy examination of the upper digestive tract.

Ectoparasites

Laemobothrion tinnunculi (Insecta, *Laemobothriidae* family) is a very large species of louse that is an obligate ecto-parasite infesting the feathers of several falcon species, many of which are endangered. These lice have also been found in birds that are used in falconry and samples have been collected from a Lanner falcon at a veterinary clinic in Dubai (Green and Turner 2005). *Pseudalloptes falconis* is another parasitic mite (*Arachnida*, *Acarina*) found on feathers of the Lanner falcon (Gaud 1983).

Parasites of the genera *Colpocephalus* (*Insecta*, *Menoponidae* family) have been found infesting individuals of *F. b. abyssinicus* and *F. b. biarmicus*. Other reported parasites include *Colpocephalus subzerafae exiguum* (in *F. b. biarmicus*), *Colpocephalus zerafae biarmicus* and *C. zerafae* (in F. b. abyssinicus – coll. Meinertzhagen n 0. 8561 BMNH, Somaliland February 1949) and '*sur la meme lame*' *C. subzerafae exiguum* and *C. zerafae biarmicus* (in *F. b. biarmicus*, BMNH coll. Meinertzhagen n. 752, Cape colony June 1909) (Tendeiro 1988).

Parsons (1974) reported a case in which an imported Lanner falcon had a massive infestation of larval ticks (*Argas* sp.). The areas of attachment showed gross lesions of excoriation, haemorrhage and necrosis. The same bird also had a heavy burden of lice, and showed damage to the bill, cere, and feet, as well as evidence of stomatitis (probably trichomonas).

Bacterial diseases

Salmonella havana (*Bacteria, Enterobacteriaceae* family) was isolated from a dead Lanner falcon embryo and was found to be resistant against isolates of spectinomycin (Battisti *et al.* 1998). Mycoplasma is known as one of the significant causes of pre-hatching mortality in birds. Among four captive breeding pairs of *F. b. tanypterus*, *Mycoplasma falconis* was isolated from the tracheas of two females during two successive years (Lublin *et al.* 2009). The use of enrofloxacin greatly reduced the embryonic mortality and during 1995–1998 fertility rates were quite high and ranged between 75 and 94% (Lublin *et al.* 2009).

Nevertheless, the rate of hatching and rearing of chicks decreased from 83% in 1995 to 20–50% in 1996–1998 (Lublin *et al.* 2009). Mortality of embryos in the egg usually occurred a few days before the end of the incubation period or on the day of hatching (Lublin *et al.* 2009). The main bacterial agents that have been diagnosed and could contribute to infection and mortality of embryos and chicks were *Staphylococci*, *Escherichia coli* and other coliforms, such as *Pseudomonas*, *Salmonella* and *Chlamydophila psittaci* (Lublin *et al.* 2009). After use of enrofloxacin (20 mg/kg Lanner falcon body weight, IP), the total numbers of eggs laid each year between 1995–2007 ranged from 15 to 28, and the percentage of fertile eggs was between 47% and 95%. The fertility rate was not affected by the antibiotic treatment and averaged 70–76%. However, hatching percentage increased significantly (p<0.05), from 47% without treatment to 70% following treatment. (Lublin *et al.* 2009).

Viral diseases

In eastern Nigeria, Newcastle disease is enzootic in poultry and of a sample of thirty-seven *F. b. abyssinicus* individuals, 57% showed high Haemagglutination-Inhibition titres (serological evidence) presumably as a result of natural exposure to the ND virus (Okoh 1979). Avian pox virus and herpesvirus infection (*Falconid herpesvirus*-1; FHV-1) has also been diagnosed in the Lanner falcon, and infection from FHV-1 in falcons is being considered to be fatal (Zsivanovits *et al.* 2004)

Fungal diseases

Aspergillosis remains a significant cause of illness and mortality for falcons (Di Somma *et al.* 2007). In addition, *Aspergillosis* is the most commonly occurring disease among wild birds that are held in captivity. Symptoms that suggest a positive diagnosis for *Aspergillus* include multiple air-sac granulomas and plaques (of around 5–10 mm in diameter), leukocytosis and heterophilia, minimal radiographic lesions, culture and cytology (Di Somma *et al.* 2007).

Undetermined respiratory disease

A number of cases of have been reported of Lanner falcons diagnosed with severe Airsaccullitis, Serratospiculiosis, Avian tuberculosis, and Hepatitis. Within the *Serratospiculum* positive group, a number of species of falcons can be affected, predominantly Peregrine falcons (51%), followed by Saker falcons (40%), Lanner falcons (5%), Gyrfalcons and Gyrfalcon hybrids (3%), and Barbary falcons (1%). Avian tubercolosis (ATB) has also been reported. Five days of treatment with Gentamicin was found to resolve a case of pneumonia in falcons (Rowley 1982). In connection with the nephrotoxicity of gentamicin (an aminoglycoside antibiotic used for bacterial infections), the measurement of N-acetyl-β-glucosaminidase (NABG) in the urine of two Lanner falcons showed increased levels. This results after the application of gentamicin, as has already been described in other species, and represents a significant increase. After repeated injections, two Lanner falcons were temporarily affected with muscle spasms, loss of balance, and loss of vision. Post-mortems have revealed incidences of avian tuberculosis in a few free living and captive Lanner Falcons in South Africa (Fernandez-Repollet *et al.* 1987).

9.7 Traumatic injuries and mortality

Collision

Although few cases of adult mortality have been recorded as a result of collisions, there are numerous reports of injury. In Pretoria, for example, a male Lanner falcon collided with a stationary car while chasing a dove across a car park five kilometres from the nest, was badly stunned, and later released back into the wild (Kemp 1993). Two individuals have been recovered after striking windows in cities in Zimbabwe and one of them (a female) had an old fracture on the left leg with pronounced rotation which may have been the result of a previous collision (Mundy and Hartley 2002). There is an increased risk of collision in urban areas, and of fourteen birds recovered for rehabilitation, nine were from urban areas (Mundy and Hartley 2002). Overall, collisions with vehicles caused two of these casualties, collisions with fences and power lines seven, and two were caused by striking windows (Mundy and Hartley 2002).

In a road survey carried out along 2,414 kilometres of highways in Cape Province, South Africa, Lanner falcons were often found dead after having been killed by cars while eating snakes (mostly *Psammophis*) and chameleons *Chamalaeleo namaquensis* (Pitman 1967). In Eastern Cape, one adult male was found dead after colliding with a fence (Stephenson 2001). One individual died following a collision with the Ovenberg power line in the Western Cape region of South Africa, but this was the only fatality found in the 199 kilometres that were surveyed (Shaw *et al.* 2010). Allan (2001) recorded the remains of one *juvenile* Lanner falcon that had apparently been killed following a collision with the Leribe-Katse power line. A wandering *juvenile* also died as the result of a collision in Veneto in Northern Italy as well a male adult in Apulia (Caldarella *et al.* 2005).

Electrocution

Electrocution is a function not only of raptor behaviour but also the structure of the power line. In one pair in the Eastern Cape, the male was electrocuted when chicks were >20 days old, and the female met the same fate after 28 days (Stephenson 2001). Fatalities have been recorded in a number raptor species as a result of electrocution and collisions with powerlines in the Northern Cape Province (Anderson 2000). Risk assessment scores for the Lanner falcon, based on morphological and behavioural data, were 3 for collision probability and 2 for electrocution, on a scale of 1 to 4 (Smallie 2011).

Drowning in reservoirs

In particularly arid areas, such as the Kalahari, raptors are more reliant on artificial water for drinking and bathing purposes, which is usually found in the form of steep-walled concrete reservoirs which are rarely full. It is believed that, the birds fall or slip into farm reservoirs while attempting to drink and they eventually drown as the walls do not provide purchase for them to climb out (Anderson 1996).

Between 1975 and 1996, at least six Lanner falcons died as a result of drowning in this way (Anderson 2000).

Bumblefoot

Bumblefoot has been recorded in the Lanner falcon, especially in captive birds, and affecetd individuals showed marked osteomyelitis of the lateral and medial trochlea of the distal tarsometatarsus, as well as of the proximal phalangial digits 2 and 3, (class IV and V bumblefoot).

Disfiguration

An immature bird found dead in South Africa had an upper mandible that curved sharply down and was twisted laterally to the right, crossing the lower mandible which had projected beyond the upper by 5 mm (Dean 1973). It had probably survived for some time by scavenging along roads in order to obtain food (Dean 1973).

Low condition

A clinical perosis case that was attributed to nutritional deficiencies was reported in a captive Lanner falcon (Perosis = *Mycoplasma* infections) the consequences of which were congestion of the parenchymal organs and a lateral bowing of the left tarsometatarsal bone (Kummerfeld 1982).

Metabolic bone disease

From radiographic analysis, the Lanner falcon could be susceptible to metabolic bone disease and urates. One Lanner falcon found with a leash entangled around its left shoulder was diagnosed with osteoarthritis.

Neoplastic disease

A squamous cell carcinoma skin papilloma has been reported in a Lanner falcon. This is essentially a benign proliferation of the epithelium (Heidenreich 1997).

Wing tip oedema and necrosis

Wing tip oedema and necrosis typically affect birds from the *Falconiformes* order, and this is generally caused when captive birds, which originate in warmer climates, are subjected to low winter temperatures. A male Lanner falcon which developed a metacarpal oedema of the right wing was treated with broad spectrum antibiotics without any need for bandaging (Lewis *et al.* 1993).

9.8 Toxicosis

It is possible that some local declines in southern Africa are associated with the treatment of seeds by chemicals containing antimicrobial or fungidal substances.

Lead

There have been reports of six captive Lanner falcons that showed radiographic evidence evidence of lead pellets or lead fragments in their gastrointestinal tracts (Samour *et al.* 2002).

Pesticides and other pollutants

Prior to 1950 two subspecies of Lanner falcon were present in Israel: *F. b. tanypterus* as a fairly common resident and *F. b. feldeggii* as a summer breeder (Mendelssohn 1972). Both have completely disappeared from the Mediterranean region, where they nested in most of the riverbed canyons in the Carmel and Galilee areas, and nowadays they can only be found in arid areas. As a consequence of the intensive use of thallium sulphate as a rodenticide, *F. b. feldeggii* has also become extinct and *F. b. tanypterus* rare and localised in the south of the country (Mendelssohn 1972). In fact, it seems that many raptor species which feed mainly on rodents have been almost entirely exterminated and other species which feed only occasionally on rodents or on grain-eating birds, such as the Lanner falcon, are slowly disappearing from large parts of Israel (Mendelssohn 1972). Impaired productivity linked to pesticide contamination and/or direct mortality caused by poisons intended to control pests is also believed to have contributed to the decline of the Lanner falcon population in southern Africa (Table 9.2; Kemp 1993; Jenkins 1997, Barnes and Jenkins 2000). Two Lanner falcons (one male and one female), trained for falconry, died from a lethal dose of insecticides. In addition, the male was stressed by the moult (Jefferies and Prestt 1966). A captive individual is known to have died as a result of Lindane poisoning, an insecticide containing a form of benzene hexachloride used as an aerosol for poultry.

Jefferies and Prestt (1966) suggested that both Peregrine and Lanner falcons are unusually sensitive to dieldrin and heptachlor epoxide, and that a combined level of these two residues in the livers of birds, at a concentration in the range 5.2–9.3 ppm, probably approached a median lethal dose for these species (Table 9.2). Overall, the prey eaten by Lanner falcons showed low pesticide content and it may be that the ingestion of only a small number of prey of species such as Woodpigeon, with a high concentrations of HEOD in their chest muscles, could be fatal (Jefferies and Prestt 1966).

Snelling *et al.* 1984 carried out a study in the Transvaal during 1969–1970 and found that concentrations based on a ppm liquid basis (DDE 308.9 ppm based on extractable fat) (n = 2), could result in a percentage change in the shell thickness index of -8.8% when compared with eggs collected before 1947, in other words prior to the use of DDT. Published data on pesticide values found in Lanner falcon eggs in Africa are listed in Table 9.2.

An adult male recovered from the non-agricultural area of Kenya was found to show no evidence of chlorinated hydrocarbon residues, while an immature bird from Nakuru killed on a road was found to contain total DDT residues of 31.2 ppm (1,114 ppm lipid weight) and dieldrin residues of 2.8 ppm (100 ppm lipid weight) which is close to the lethal risk level (Frank *et al.* 1977).

	DDE	DDT	HEOD	Developmental condition
North West Province	21.6[1] – 83.4[2] – 288.0[3]		Trace	
Pretoria	17.2[1] – 66.3[2] –- 229.8[3]		No data	No development
Mpumalanga	–	13.62[2]	7.19[2]	Fertile
Zimbabwe	4.24[1]		0.83[1]	Infertile
Durban	6.24[1]		1.84[1]	

Table 9.2 Contaminants found in the eggs of Lanner falcons in southern Africa. 1 = Based on 74% water for eggs, 2 = Residue levels are expressed on a dried weight basis, 3 = based on extractable fat (Peakall and Kemp 1976, Tannock *et al.* 1983, Snelling *et al.* 1984).

An immature Lanner falcon captured in the North Western Province of South Africa was found to have a very high ΣDDT (total DDT = DDT + DDE + DDD) concentration (15.73 µg l^{-1}), and a high value of dieldrin (30.65 µg l^{-1}) (Smith and Bouwman 2000). Mendelsohn (1972) found that bird-eating raptors such as the Lanner falcon tended to be more susceptible to contamination than mammal-eating raptors. In addition, he calculated a DDE egg concentration of 193.93 µg kg^{-1} which was almost three times higher than that found in raptor species that preyed on mammals, invertebrates, and lizards (Smith and Bouwman 2000).

Currently, there are insufficient data to evaluate the demographic effects of pesticide poisoning (Movalli *et al.* 2008). Kemp (1993) attributed the local extinction of Lanner falcons in his study area to the east of Pretoria to a combination of reduced fecundity and increased mortality, possibly linked to the use of poisonous seed dressings in maize fields.

The sole study regarding pollutants and their effects on *F. b. feldeggii* was recently completed in Sicily (Movalli *et al.* 2008). Data included blood and tissue samples taken from Lanner falcon chicks as well as from the most important prey species (*Pica pica* and *Columba livia*) in order to evaluate the bioaccumulation of contaminants through the food chain (Movalli *et al.* 2008). The blood of Lanner falcon chicks appeared to be free of Organochlorine compound pesticide residues above the detection limits, and free of PCB residues except for one solitary sample of PCB153 (21.8 ng g^{-1} wet weight; Movalli *et al.* 2008). On the other hand, DDE (a metabolite of DDT) was detected in 30 of the 46 samples. DDE was found in 40 % of *C. livia* samples and in 72 % of *P. pica* samples, but the values were under critical levels except for a few individuals of Magpie (10%) which may have had exceptional levels of DDE residues. In addition, the HEOD levels in Lanner falcon prey shows an almost normal distribution and it seems that neither species is particularly important as a potential source of HEOD in the food chain (Movalli *et al.* 2008).

9.9 Illegal trade of eggs and birds

Human persecution, and the collection of eggs and nestlings for falconry, appear to be the main threats to the species in the Middle East with, for example, more than one hundred individuals trapped annually on the Yemeni side of the Bab al Mandab straits (Shirihai *et al.* 2000). In September 2014, 142 large falcons (Lanner and Barbary falcons) were recovered by police and the Red Sea Protectorates from poachers on their way to Sharqiya (Figure 9.1). There remains an opportunistic trade in wildlife through the Sana'a's Nuqum animal suq in Yemen, where it is frequently possible to find Lanner falcons for sale (Stanton 2010).

Nest robbing takes place in several areas of Macedonia, including along the Pčinja Petrošnica Kriva Reka rivers, in the Osogovo Mountains, around Lake Mantovo, and near the Kriva Lakavica river (Velevski *et al.* 2010). In Italy in 1967, Lanner falcons were still sufficiently abundant that a German falconer could collect twenty-three young (Bijleveld 1974). This practice was also prevalent in Emilia-Romagna during the 1970s (Chiavetta 1982). The species often therefore became threatened or locally extinct through the demands of falconers, which appears to have happened in areas such as Sudan and in the Arabian Peninsula (Brown *et al.* 1982). In Sicily, there remains a certain degree of pressure on *F. b. feldeggii* from this source, but there are insufficient quantitative data available in order to evaluate the impact of the loss of eggs and chicks on the viability of the population.

9.10 Conservation issues

F. b. feldeggii is the most threatened of the Lanner falcon races and the European Union has produced an International Action Plan for its conservation. This plan also covers *F. b. erlangeri* and *F. b. tanypterus* that are present in Mediterranean countries (Gustin *et al.* 2002). An Italian Action Plan has also been initiated by the Italian Minister for Environmental Protection due to the relative importance of the Italian populations for the global conservation of the *F. b. feldeggii* subspecies (Andreotti and Leonardi 2007). It is listed as an endangered species in Annex I of the Birds Directive and classified as "*endangered*" at the European level by BirdLife International. It is also classed as a category 3 Species of European Conservation Concern (SPEC3), as it is experiencing rapid decline (Andreotti an Leonardi 2007). *F. b. feldeggii* is also listed in Appendix II of the Bonn Convention, Appendix II of the Bern Convention, and Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; Andreotti and Leonardi 2007). Globally, however, it is classified as a species of Least Concern (LC) due to its widespread distribution and relative abundance in the Afrotropics (IUCN 2012).

Although *F. b. biarmicus* has been described as relatively common across southern Africa (in South Africa, Lesotho, and Swaziland), it has recently been listed in the Red Data Book as a near-threatened species (Barnes and Jenkins 2000). Population declines have been observed in the region, particularly in Lesotho and Swaziland, in areas of intensive agriculture in the grassland biome, possibly linked to the use of agro-chemicals (Barnes and Jenkins 2000).

Despite the fact that *F. b. feldeggii* has been legally protected in Italy since 1977, the breeding population has not increased in numbers as has been observed for other raptor species such as the Golden Eagle and the Peregrine falcon (Andreotti and Leonardi 2007). This is probably due to the fact that in Italy *F. b. feldeggii* lives at the edge of its distributional range in the Palearctic, with only small isolated population demes (of around 3–10 pairs), and it is therefore more vulnerable (Andreotti *et al.* 2008).

The conservation measures adopted in Italy are in many ways inadequate, given that only 23–28% of breeding pairs are resident in protected areas. In fact, the preferred habitats of *F. b. feldeggii*, such as steppe, pastureland, scrublands, and abandoned fields are not well represented in the protected areas that have been established to date (Andreotti *et al.* 2008). In Macedonia, for example, a much higher percentage of the Lanner falcon population, around 50%, lives inside areas designated as Important Bird Areas (Velevski *et al.* 2010).

Captive breeding

The large captive falcon programme which was conducted at Cornell University during the 1970s produced several young of the *F. b. biarmicus* race from parents which had been brought from South Africa (Table 9.3; Snelling 1973, Cade *et al.* 1977). In particular, breeding by F1 individuals (more than eight breeding females) produced twenty-seven young between 1972–1976 (Cade *et al.* 1977). During the same period, captive birds of the *F. b. erlangeri* race also produced a number of young (J-F. Terrace quoted in Snelling 1973). The incubation period in captivity was found to be 32 days, which is shorter than the 35 days more usually seen in the wild (Snelling 1973). A post-mortem examination of a chick that died in captivity was found to exhibit a gross *Aspergillus* infection in the lungs. This infection is generally caused by a fungus that is often present in the air, but generally only attacks weakened birds (Snelling 1973). Another notable cause of mortality was the unretracted yolk sac (Snelling 1973).

Generally, the exchange of large size food items between birds stimulates the '*pair + bond feeding*' relationship. In similar situations in captivity, quarrelling was often observed between Lanner falcons. It has been suggested that this behaviour therefore possibly does not occur in the wild, whereas quarrelling between birds in captivity was sometimes quite serious (Olwagen and Olwagen 1984). During breeding attempts in captivity, the female often made a nest scrape and exhibited brooding behaviour but was openly aggressive to males (Snelling 1973). However, there was an abrupt change in behaviour when the female was 3.5 and the male 2.5 years old, when aggression ceased, copulation occurred, and the first egg was laid ten days later. Seven eggs were subsequently laid in a three-day interval (Snelling 1973).

Reintroduction projects

The sole reintroduction project involving Lanner falcons was carried out in Israel at Ramat HaNadiv, which is located at the southern end of Mount Carmel (Getreide and Hatzofe 1990, Hatzofe 2001, E. Bartov and O. Hatzofe unpl. typ.). A breeding nucleus of captive *F. b. tanypterus* was established at the Tel Aviv University Research

	1973	1974	1975	1976	Total
Number of laying females	2	1	1	1	
Number of fertile females	2	1	1	1	
Total eggs laid	12	11	8	10	41
Number of fertile eggs	9	10	8	10	37 (90%)
Number of eggs hatched	6	8	6	8	28 (68%)
Number of young raised	6	7	6	8	27 (66%)

Table 9.3 Egg production in captivity by a female *F. b. biarmicus*. Infertile eggs amounted to 10% and pre-hatching failures 32%. After these crucial stages the loss of young was only 1% (Cade *et al.* 1977).

Zoo and in the Nature Gardens of the SPNI in Abu Kabir (Hatzofe 2001). The source population came from individuals that had been held in captivity at the zoological gardens, having originally been captured in the Judean Desert and eastern Samaria, as well as one from an egg collection that had been gathered from a nest in the wild (Hatzofe 2001). Nestlings of 28–30 days old were transferred to an artificial nest located on a cliff, and remained inside for about two weeks until they reached their natural fledging age 44 days after hatching (Hatzofe 2001). Nestlings were subsequently supplied with food without any direct human contact. When they were large enough they were ringed with identification rings (metal and coloured) and fitted with backpack radio transmitters which weighed around 15–20 grams (Hatzofe 2001). Sixty-one Lanner falcons have been released in this way on the Carmel since May 1990, and fourteen more have been released in Nahal Kziv in the Galilee region (Hatzofe 2001).

The first nesting attempt by reintroduced Lanner falcons was in 1999 at the Hadera power station by a pair released from Ramat HaNadiv (the male in 1995 and the female in 1997). The pair appeared to produce a single nestling but it fell out of the nest at an age of 38 days. It was recovered and released together with three captive nestlings and the parents re-adopted it, eight kilometres from the original nest (Hatzofe 2001). The high survival rate of released individuals suggests that it is possible to re-establish a stable population in the Mediterranean region of Israel with the release of only another 100 individuals over the course of five to seven years (Hatzofe 2001).

Nest boxes

As a conservation measure, the Italian Action Plan for the Lanner falcon proposed the use of nest boxes in areas with a lack of suitable cliff sites (Andreotti and Leonardi 2007). Nest boxes in Harare in Zimbabwe were regularly used by pairs of Lanner falcons for at least five years. These consisted of a shallow wooden tray (50 × 50 × 10 cm) filled with washed pea gravel (Deacon *et al*. 2002).

Rehabilitation centres

There have been very few recorded cases of *F. b. feldeggii* individuals recovered in Italy, which may be due to its scarcity in the field. In fact, only three individuals were recovered in rehabilitation centres in Campania (Southern Italy) between 2000–2005 and five individuals (two *juveniles*) in Foggia province (Apulia; Caldarella *et al*. 2005).

Chapter 10.
Lanner, Laggar, Black and Grey falcons

10.1 Introduction

The *Hierofalco* group can be characterized by the broad genetic and morphological similarities between its members (see Chapters 1-3). Before the use of modern genetic tools, features such as size and plumage characteristics played a fundamental role in the inclusion or exclusion of several falcon species within this subgenus (Kleinschmidt 1901). In fact, evolutionary convergence in plumage patterns and habits of the so-called '*desert falcons*' increased the size of this group through the inclusion of several species of large falcon from all of the continents (White 1996). For example, the Red-naped Shaheen *F. p. babylonicus* was considered by H. Schegel as being a typical '*counterpart*' of the Lanner falcon in inner Asia from beyond the eastern limits of the range associated with Hierofalcons (Bree 1859, Dresser 1871–1881, Martorelli 1911).

A new genetic analysis made by Fuchs *et al.* (2015), revealed an early divergence

Figure 10.1 Perched adult Laggar falcon *Falco jugger* (Rajastan, India). © and courtesy of Sunil Kini.

of three species that are usually considered to have uncertain affinities, the Red-necked falcon, Prairie falcon *F. mexicanus*, and Grey falcon *F. hypoleucos*. The next divergence is between clades for the Peregrine group and the Hierofalcons including the Lanner falcon, Laggar falcon, Saker falcon, Gyrfalcon, and Black falcon *F. subniger* (Fuchs *et al.* 2015). The overall genetic divergence between these species was found to be low, especially in the species that are not monophyletic, such as the Lanner falcon, Saker falcon, and Gyrfalcon (Fuchs *et al.* 2015). Chapters 1, 2, and 3 explore the genetic, morphological, and historical biogeographical relationships between these species. This chapter will focus on the ecological and behavioural similarities between the Lanner falcon and two closely allied species, the Laggar and Black falcons, and one of the uncertain affiliate species, the Grey falcon. Interestingly, all of these species suffer from a distinct lack of detailed information concerning their main biological traits across different parts of their distributional ranges (Leonardi 2001, Naoroji 2006, Debus and Olsen 2010, Schoenjahn 2013).

10.2 Laggar falcon

The Laggar falcon is the ecological counterpart and geographical replacement for the Lanner falcon in India (Naoroji 2006). In common with the Lanner, the Laggar falcon prefers arid to semi-arid open areas such as scrubland, grassland, or thin dry-deciduous forested areas (Figure 10.1; Naoroji 2006). These two species are separated by a large geographical area which includes Pakistan, Afghanistan, and south-eastern Iran. In Afghanistan, where the Laggar falcon could be considered as a rare passage migrant, no sightings of the Lanner falcon have been reported (Naoroji 2006). This is also the case in Pakistan where the Laggar falcon is a rare resident (Naoroji 2006). In fact, its breeding range extends west to around 64°E in Pakistan, Balochistan, and into eastern Afghanistan, but it also known to occur as a vagrant as far west as Iran, and as far north as southern Kazakhastan and Uzbekistan, without any evidence of breeding. Both falcons prefer to hunt prey through the use of swift low-level attacks or through stoops from soaring flights. Interestingly, the Laggar falcon employ cooperative hunting, with one bird flushing prey towards its mate, a technique that is also known to be used by the Lanner falcon (Leonardi 1999, Naoroji 2006). The prey preferences of the Laggar falcon are also very similar to those of the Lanner falcon and consists mainly of small birds, but both species will also hunt mammals, reptiles, and invertebrates (Gnamaselvan and Natarajan 1994). The Laggar falcon is known to occasionally feed on bats as well as on flying insects such as termites, behaviour which has also been observed in both *F. b. biarmicus* and *F. b. abyssinicus*, (Thomsett 1987, Gnamaselvan and Natarajan 1994). In common with *F. b. biarmicus*, the Laggar falcon is also known to feed on domestic poultry when it is available (Barbour 1971, Gnamaselvan and Natarajan 1994). In desert and

Plate II


5 cm
Lanner falcon
Laggar falcon
© Marco Preziosi
Saker falcon
Gyrfalcon

arid habitats, the primary prey of the Laggar falcon is the Indian Spiny-tailed Lizard *Saara hardwickii*, which is a similar relationship to that observed between *F. b. erlangeri* and the Bell's Dabb Lizard *Uromastyx acanthinura* (S. Kini pers. comm., Heim de Balsac and Mayaud 1962). Preferred nest-sites of the Laggar falcon include rocky cliffs and outcrops, but it also nests on man-made structures such as buildings, pylons, and forts, as well as in trees using the abandoned nests of Corvids, Storks, and other large raptors (Naoroji 2006).

10.3 Black falcon

The Black falcon is Australia's representative of the subgenus *Hierofalco* and ecologically and morphologically it is closest to the Laggar falcon (Debus and Olsen 2010, Fuchs *et al.* 2015). The Black Falcon prefers to breed in old Raven *Corvus* sp. nests, usually in *Eucalyptus camaldulensis* trees or on electricity pylons, but is not known to breed on rocky cliffs (Debus and Olsen 2010). Availability of nest sites may therefore be a limiting resource for Black falcons (Debus and Olsen 2010). Avian prey constitutes the bulk of the diet of Black falcons and the common and widespread Galah *Eolophus roseicapillus* is one of the most frequent prey species (Debus and Olsen 2010, Charley *et al.* 2014). Interestingly, as is the case with the Lanner falcon, the Black falcon can exploit mammals when they are particularly abundant (Debus and Olsen 2010). In arid habitats there is much dietary overlap between the Black and Grey falcons (Debus and Olsen 2010). In common with the Lanner and Laggar falcons, the Black falcon hunts cooperatively for medium-sized prey such as pigeons and quails, and is also known to hunt bats (Charley *et al.* 2014). Overall, the Black falcon shares the same tendency as the Lanner and Laggar falcons to shift, when necessary, from a purely avian diet to a more varied choice of prey including mammals, bats, reptiles, and insects (Chapter 7; Gnamaselvan and Natarajan 1994, Charley *et al.* 2014). The Black falcon has a similar vocal repertoire to the Lanner falcon (Leonardi *et al.* 2013, Charley *et al.* 2014). As has been reported for the Lanner falcon, the frequency of vocalisations of male Black falcons shows a correlation with fledging success in breeding pairs, in contrast to the lower fledging success seen at sites where males vocalise less frequently (Leonardi *et al.* 2013, Charley *et al.* 2014).

10.4 Grey falcon

The Grey Falcon is an elusive species with very low density throughout its vast distributional range in Australia, with a preference for remote habitats (Schoenjahn 2013). A comprehensive study revealed that 70% of nest sites were on repeaters, 22% in trees, and 4% on pylons (Schoenjahn 2013). As is the case with the Black falcon, the Grey falcon does not use rocky cliffs as breeding sites. The Grey falcon is a specialized forager and its diet consists of 99% birds and 1% small mammals (Schoenjahn 2013, Janse *et al.* 2015). The main factors that seem to contribute to the scarcity of the Grey falcon are its habitat preference for regions of high annual average temperatures, combined with its restricted dietary preferences (Schoenjahn 2013). The unpredictability and the extreme climate that characterise such environments may render some parts of the breeding distribution periodically unfavourable to the species. The climate in these regions is also linked to the limited availability of prey, a factor that is further accentuated by the limited dietary flexibility of the species (Schoenjahn 2013). Interestingly, 95% of recorded breeding events are in zones where the mean annual rainfall is <500 mm (Schoenjahn 2013). The amount of rainfall in the pre-breeding months seems to have a positive effect on the productivity of the Grey falcon, presumably through an increase in prey availability in the months following hatching (Janse *et al.* 2015).

10.5 Ecological and behavioural similarities

As might be expected, the Laggar falcon is closely related to the Lanner falcon in several aspects of its behaviour, and it seems to show a much stronger affinity with the nominate race than with the other races (Table 10.1). Although this is a descriptive analysis, this similarity is consistent with genetic evidence and with the presumed sequence of colonization (see Chapter 3). The Black falcon has recently been confirmed as part of *Hierofalco* group, and shows many behavioural similarities, such as cooperative hunting and the ability to exploit alternative prey, with the Lanner and Laggar falcons (Table 10.1). Nevertheless, neither the Laggar falcon or the Grey falcon breed on cliffs. The Grey falcon is also effectively a specialized predator of birds (Table 10.1). These behavioural and ecological aspects may reflect the proposed genetic distance between the species which is due to an early sequential divergence.

	1	2	3	4	5	6	Total
F. b. feldeggii	•		U		U	•	B-(M-R-I)
F. b. erlangeri	•	•	•		•	•	B-(M-R-I)
F. b. tanypterus	•	•	•			•	B-(M-R-I)
F. b. abyssinicus	•	•				•	B-(M-R-I)
F. b. biarmicus	•	•	•	•	•	•	B-(M-R-I)
F. jugger	•	•	•	•	•		B-(M-R-I)
F. subniger	•	•	•		•	•	B (M-R-I)
F. hypoleucos			•		•		B (M)

Table 10.1 Comparison of foraging behaviour and breeding biology between Lanner, Laggar, Black, and Grey falcons. 1 Cooperative hunting, 2 Bat-hunting 3 Nest sites on man-made structures (pylons, ruins) 4 Urban nest sites, 5 Tree nests, 6 Cliff nests, 9 Diet: B = birds, M = mammals, R = reptiles, I = invertebrates; U = Uncommon

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The Lanner falcon

This book provides a worldwide review of the ecology, behaviour, morphology, and breeding biology of the Lanner falcon *Falco biarmicus*. From historical sources to the most recent ornithological literature, a comprehensive approach reveals the uniqueness and adaptability of this falcon that ranges from the Afrotropic to the Palearctic ecozones.