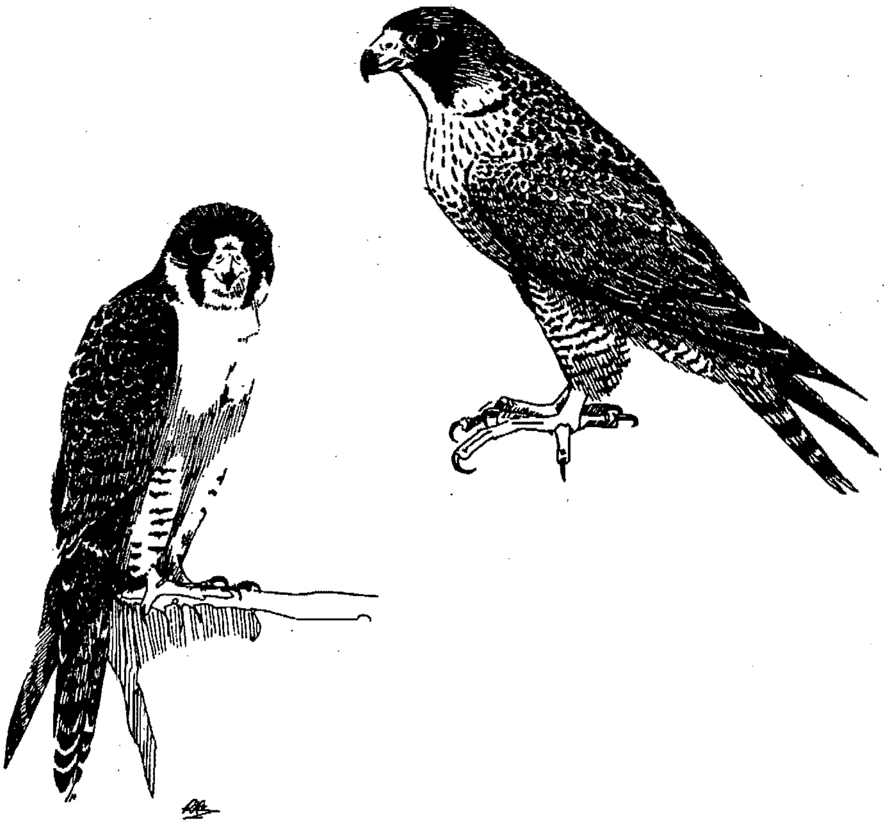
Behavioural ecology of Peregrine and Lanner Falcons in South Africa

Andrew Robert Jenkins



Thesis submitted for the degree of Doctor of Philosophy

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Contents

Drawings and sketches by Rob Davies

Abstract

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The Peregrine Falcon *Falco peregrinus* is a specialized predator of birds. It occurs almost worldwide but is generally uncommon. In many areas, it is sympatric with one of a complex of similar, less specialized, congeneric species (subgenus *Hierofalco*, the desert falcons). Peregrine density and productivity tend to decrease with latitude, while desert falcons may be most successful in the tropics. This study compares the biology of Peregrines and sympatric Lanner Falcons *F. biarmicus* in South Africa, and examines the relative influence of resource limitation and interspecific competition with congeners on the natural regulation of Peregrine populations in tropical environments.

In a quantitative analysis of distribution, Lanners were more widely distributed than Peregrines in South Africa, and generally outnumbered them by at least 10:1. Peregrines were largely restricted to high cliff areas, and were most frequent in the Fynbos biome in the temperate southwest. Lanners were less constrained by topography; breeding birds favoured the eastern grasslands, but numbers moved into the flat, arid Karoo and Kalahari in the non-breeding season. Elevation, nest ledge size, cliff size and the structure of scree slope vegetation were the main variables distinguishing nesting habitats typical of each species, and of Peregrine populations in different parts of the country. Peregrines used larger nest ledges on higher cliffs than Lanners, and temperate Peregrines used smaller ledges on lower cliffs than Peregrines in the subtropics.

Morphometric differences between Peregrines and Lanners (Peregrines have higher wing loading and larger feet) predict differences in flight performance, energetics and food handling abilities. These were largely confirmed in the field: Peregrines flew faster, flapped more, used thermals less and made more strikes from perches at aerial prey than Lanners using the same habitat. On average, South African Peregrines spent 30-50% of the day in the vicinity of the nest cliff, and made about 0.5 strikes per hour in the immediate area. Most strikes were made from perches high on the cliff, and pairs occupying higher cliffs were more successful hunters. The height difference between perched Peregrine and propsective prey at the start of a hunt was positively correlated with strike success.

Aspects of the diet and breeding biology of small, sympatric populations of Peregrines and Lanners were compared in a tropical area (Soutpansberg), and tropical Peregrines were compared with subtropical (Orange River) and south temperate (Cape Peninsula) populations. Both species preyed mostly on birds. Columbids and other aerial or 'commuter' species comprised the bulk of Peregrine prey throughout. Cape Peninsula Peregrines had the least diverse diet, and took more juvenile birds than Peregrines in the other two areas. Soutpansberg Lanners took mainly open-country, terrestrial or cursorial species, including a high proportion of young domestic fowl. Sympatric Peregrines took mainly woodland or cliff-dwelling species. Diet overlap was about 35%, and close neighbouring pairs of congeners did not affect food-niche width of either species.

Parental care at nests was compared using time-lapse photography and direct observation. Accounting for the effects of brood size and age, the quality of parental care provided by Cape Peninsula Peregrines and Soutpansberg Lanners (in terms of provisioning rates and adult attendance at the nest) was superior to that of Soutpansberg Peregrines. Also, female participation in the foraging effort was greatest by Soutpansberg Peregrines, which may have compromised nest security. Breeding success of Peregrines was lowest on the Cape Peninsula and highest on the Orange River, although the Cape Peninsula population achieved the highest productivity in any one year. Fledging rates of Soutpansberg Peregrines and Lanners were not significantly different, although Lanner productivity was consistently higher. Close neighbouring pairs of congeners did not affect the breeding performance of either species. Egg and hatchling mortality increased with spring rainfall on the Cape Peninsula. Generally, breeding success of South African Peregrines reflected flutctuations in the physical environment which themselves influenced prey availability.

Evidence from this study suggests that Peregrine populations in the tropics are limited by resource deficiency and not by proximate competition with sympatric congeners. Morphological and behavioural specialization may restrict Peregrines to optimal foraging habitats (high cliffs) in areas where prey are not concentrated or particularly vulnerable to predation. Prey availability, and hence habitat specificity, density and productivity, may be profoundly influenced by latitudinal trends in the length and synchrony of avian breeding seasons. Populations of other widespread but specialized raptors may be similarly controlled. Food limitation in the tropics has led to specialization and rarity in Peregrines, and generalization and relative abundance in desert falcons.

Acknowledgements

This project could not have been completed without the unflagging faith and endless moral and financial support of my parents, Harold and Bridget Jenkins. I can only hope that the end (finally) justifies the means, and thank them sincerely for giving me the opportunity to pursue my dreams.

Zelda Bate stood by me through heavy weather, and was still there, smiling, when the sun came out. Her patience and tolerance were an inspiration, and she never resented my obsession with the birds. She was my comfort in the field, my backbone when resolve failed and my common-sense on many cotton-wool days.

Dave Allan and Chris Brown did much to influence and encourage my early interest in raptors, and were never short of a vac job to occupy my school and varsity holidays. Dave was always available to discuss perries and to share his experiences, data and ideas during the initial stages of the study. He introduced me to the Soutpansberg and the escarpment, and somehow got me in at the Fitz.

Tim Wagner and Ian Hoffman of the Gauteng Falconry Club were the first to survey the Soutpansberg cliffs and kindly shared their hard-earned knowledge with me. Despite our fundamental differences, Tim and I found found common ground in our passion and enthusiasm for peregrines. We spent many Soutpansberg days battling the heat, the thorns and the gradient in our search for falcons, and for the privilege of watching the wasp at work.

Thanks to Roy Siegfried for recognizing the potential of this project and for letting me run with it, often against his better judgement. Phil Hockey supervised the latter stages of the study and red-penned many manuscripts. Alan Kemp, Rob Simmons and Rob Davies gave readily of their considerable expertise, usually by return post. Rob Davies' input on the construction of time-lapse cameras was invaluable, and he kindly provided many of the sketches and drawings which decorate this thesis free of charge. Graham `Bones' Avery pored over and identified more bird bits than seemed humanly possible.

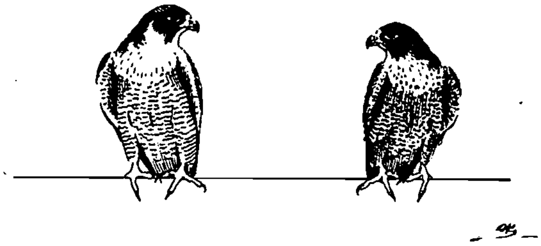
Of my varsity colleagues, Gerard Malan and Anthony van Zyl were always keen to talk the hawks and walk the walks, and we shared many bird and bakkie experiences. Gerard patiently guided me through a number of statistical mazes, and got me up and running on the vax. Helen de Klerk and Jane Turpie kept me going at the end, Andrea Plös provided technical support beyond the call of duty, and Felicia Stoch helped me make pages.

Many thanks to the Greaves family of Buzzard Mountain Retreat for their warm hospitality during field seasons in the Soutpansberg, to Koos de Goede for his stoic efforts to protect Peregrine sites in the northern suburbs of Cape Town and for reminding me to put the welfare of the birds first, and to the management and staff of the Athlone Power Station who went more than the extra mile to accommodate both peregrines and attendant biologist.

The administrators and staff of South African National Parks and the Cape Metropolitan Council kindly allowed me to conduct research in the Augrabies Falls National Park and the Silvermine and Cape of Good Hope Nature Reserves respectively.

During the course of this project I received funding from the Foundation for Research Development, the Leslie Brown Memorial Grant (administered by the Raptor Research Foundation), the Gordon Sprigg Scholarship, the Duncan Campbell Actuarial Bequest and the Raptor Conservation Group. Particular thanks to Steve Phelps of Peregrine Properties for his generous financial support over the last three years of the study.

Additional contributors to particular sections of the project are acknowledged at the end of each chapter.



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General Introduction

"For ten years I spent all my winters searching for that restless brilliance that peregrines flush from the sky." (J.A. Baker, The Peregrine, *Harper & Row 1967).*

"The Peregrine is, in fact, a fascinating subject for scientific study...there are many deeper aspects [of its natural history] *which remain as puzzles for others to solve." Derek Ratcliffe,* The Peregrine Falcon, *T & AD Poyser 1993).*

This thesis is the culmination of a long-standing ambition to study peregrines; it is an end in itself rather than simply a means to a higher qualification. The charisma of the falcons held me enthralled throughout, and at no stage were my efforts motivated primarily by academic achievement. I watched because I wanted to witness, and recorded and analysed because I wanted to understand.

Development and rationale of the study

The Peregrine Falcon *Falco peregrinus* is a small to medium-sized raptor which feeds mainly on other birds, caught in high-speed aerial strikes (Cade 1982, del Hoyo *et al.* 1994). Peregrines are monogamous and territorial, and pairs generally breed on cliffs but may nest in trees and even on the ground in some areas. The species comprises about 20 races, with a combined distribution which covers most of the major land masses and islands of the world (Cade 1982, del Hoyo *et al.* 1994). Given its celebrated prowess as a predator and its capacity to inhabit a great diversity of environments, the Peregrine is surprisingly uncommon throughout most of its range (Beebe 1974, Cade 1982, Cade *et al.* 1988). In the present study, I hope to contribute to an understanding of this distributional paradox.

Falcons in Africa

Peregrines are generally rare in Africa (Cade 1969, Brown *et al.* 1982, Mendelsohn 1988), although reliable data on distribution and abundance are few. The breeding biology of the African Peregrine *F. p. minor* has been studied at one site in central Zimbabwe (Hustler 1983), and falcon research is ongoing in that country (e.g. Hartley 1992, 1995). In addition, population surveys are available for parts of Kenya (Thomsett 1988), the Waterberg Plateau, Namibia (Brown & Cooper 1987) and the Western Cape Province (Pepler *et al.* 1991) and the former Transvaal, South Africa (Tarboton & Allan 1984). The latter study found that resident pairs were restricted to high cliffs or cliffs overlooking continuous woodland, possibly because these habitats provide optimal conditions for cost-effective perch-hunting in the vicinity of the nest. The connection between the specialized foraging methods of the Peregrine, the physical structure of its environment and the distribution of breeding pairs was first articulated by Beebe (1974), but its application to African Peregrines (Tarboton 1984) was novel.

Tarboton's hypothesis initiated my interest in the factors limiting Peregrine populations in South Africa. I spent some time as an undergraduate in 1986 watching

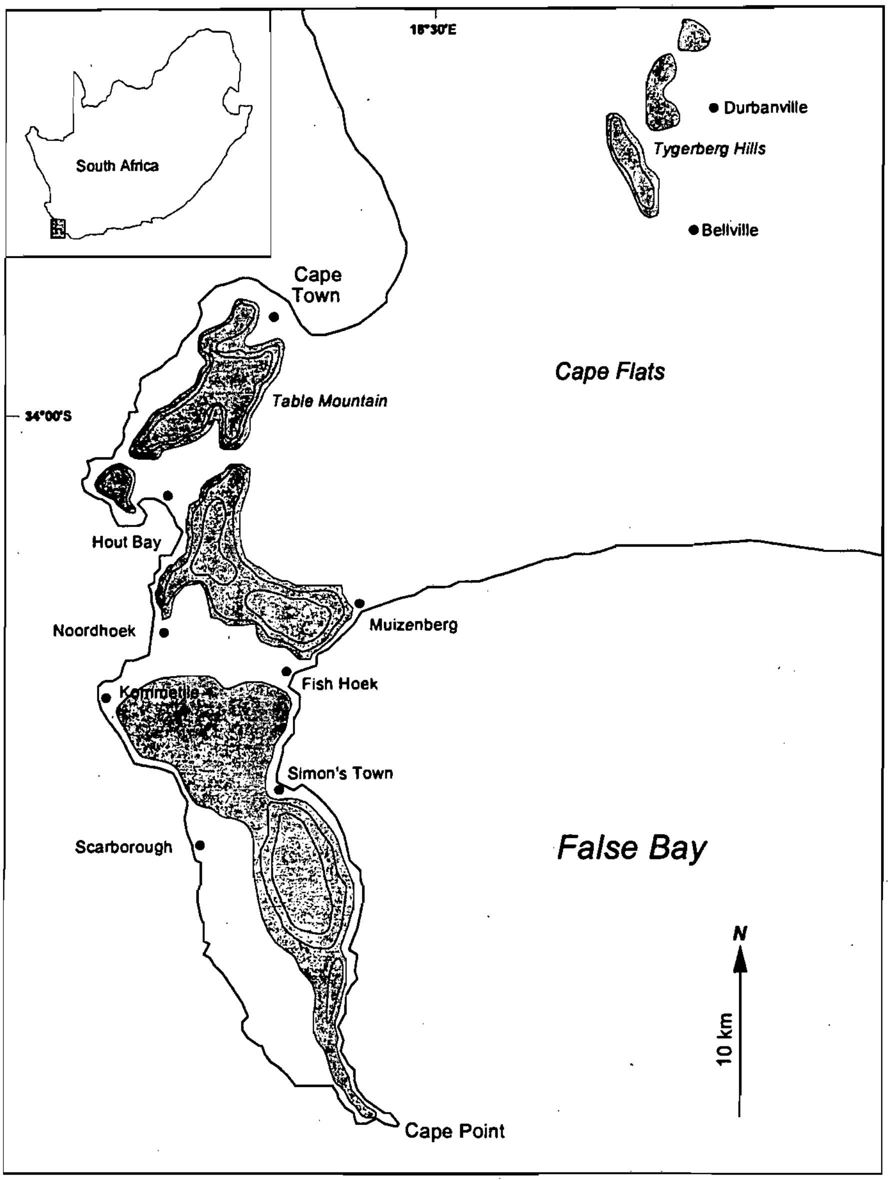


Figure 1 Location and basic geography of the Cape Peninsula study area. Shading denotes areas of high relief.

a pair of Peregrines at a high cliff site on the Cape Peninsula to investigate the relative importance of the cliff and its surrounds in the falcons' foraging activities. The data I obtained were limited, the results equivocal, and their publication (Jenkins 1987) prompted some criticism (Hustler 1988, and see Jenkins 1988). However, I gained valuable experience in the field, and established sufficient credibility to continue my research as an M.Sc. thesis on habitat selection by Peregrines in South Africa, which I began in 1989.

Comments on the relative status of the Lanner Falcon *F. biarmicus* in the Afrotropics have pervaded most of the published work on African Peregrines (e.g. Tarboton 1984, Thomson 1984, Mendelsohn 1988). Closely related and morphologically and ecologically similar, the Lanner is common in many parts of Africa (Brown *et al.* 1982), and seems relatively free from the environmental constraints which limit the Peregrine. Largely descriptive accounts have attributed the Lanners' success to its less specialized foraging habits and its ability to exclude Peregrines from otherwise suitable habitat (Thomson 1984, Tarboton & Allan 1984, Brown & Cooper 1987). Data on the biology of its more successful (but little known) relative are obviously vital to any study of African Peregrine distribution. By introducing this comparative component to my study I was able to upgrade my research to Ph.D. level in 1991.

Global perspectives

The Peregrine's extensive distribution, and the wealth of data available on the biology of populations around the world (e.g. Cade *et al.* 1988) make it an attractive option for comparing life-history traits on a global scale. Latitudinal trends in Peregrine clutch and brood sizes generally comply with established patterns, with reproductive output higher in the temperate and Arctic zones than in the tropics (Court *et al.* 1988, Jenkins 1991, although see Hickey 1969, Mendelsohn 1988). However, a closer look at the literature suggests that

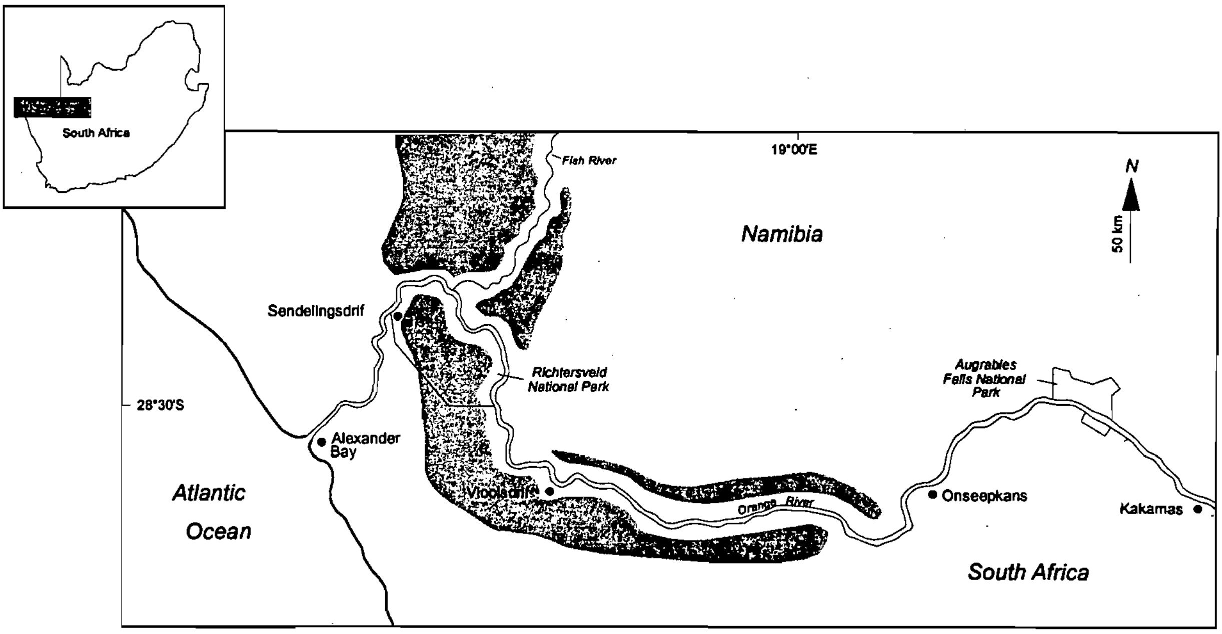


Figure II Location and basic geography of the Orange River study area. Shading denotes areas of high relief.

population density also decreases with latitude, and that breeding pairs are increasingly restricted to optimal habitats (higher cliffs) with proximity to the Equator (Jenkins 1991). Hence, conditions which limit Peregrine populations in the Afrotropics may prevail in all tropical areas.

In the absence of any obvious association between cliff habitat availability and latitude, I looked for possible, broad-scale trends in prey availability which could explain this distribution pattern. A fundamental difference between populations of small birds in the tropics and those at higher latitudes is the average length and productivity of breeding seasons. Temperate and Arctic conditions restrict avian breeding to a short season with a high total output of young. More stable tropical conditions are typically associated with more diffuse seasons, with smaller clutch and brood sizes (Immelmann 1971, Ricklefs 1980, Wyndham 1986). Perhaps the absence of a temporally concentrated prey breeding effort in the tropics with its associated flush of vulnerable, newly-fledged young as an easily exploitable prey base, restricts Peregrine pairs to those habitats which particularly favour their specialized hunting methods? This hypothesis (Jenkins 1991) has been central to the development of my thesis, and infers that African Peregrines are limited by resource availability rather than by competition with Lanners. The corollary is that Lanners are successful in Africa because they are less stereotyped foragers, which is advantageous in more stable environments.

Most of the larger members of the genus *Falco* fall into one of two subgenera, *Rhynchodon* (the peregrines) and *Hierofalco* (the desert falcons) (Cade 1982). *Rhynchodon* consists of one species, the Peregrine, with its wide distribution. The distribution of *Hierofalco* is also extensive, but comprises five discrete species of the which the Lanner is one. Collectively, the hierofalcons are sympatric with the Peregrine over much of its range, and they are morphologically and behaviourally less specialized. The available data suggest that in areas of sympatry, Peregrines are more successful and numerous in Arctic and temperate environments, but they are outnumbered by desert falcons at lower latitudes (Porter & White 1973, Brown *et al.* 1982, Cade 1982, Cade *et al.* 1988, Poole & Bromley 1988, Manzi & Perna 1994, del Hoyo *et al.* 1994). Thus, the African Peregrine/Lanner comparison may have wider relevance to large falcon distributions globally.

Objectives and outline of the study

The immediate aim of this study is to determine the extent of differences in the distribution and abundance of Peregrines and Lanners in South Africa, and to establish possible reasons for these differences. Specifically, the study investigates whether Peregrines are resource-limited, and if so, what is the nature of this limitation, and is it independent of the presence of Lanners? More generally, the wide distributions of large falcon taxa, coupled with apparent contrasts in foraging ecology, present an opportunity to examine the relationship between resource availability, niche width and population status. While this study was driven by discrete starting hypotheses, the limitations imposed by the elusive nature and scarcity of the birds, and the ruggedness of their preferred habitats, denied any realistic possibility of actively testing these hypotheses by experimentation and manipulation. Instead, the emphasis was on carefully compiling sufficient observational data to either support or falsify predictions.

Every effort was made to communicate data and

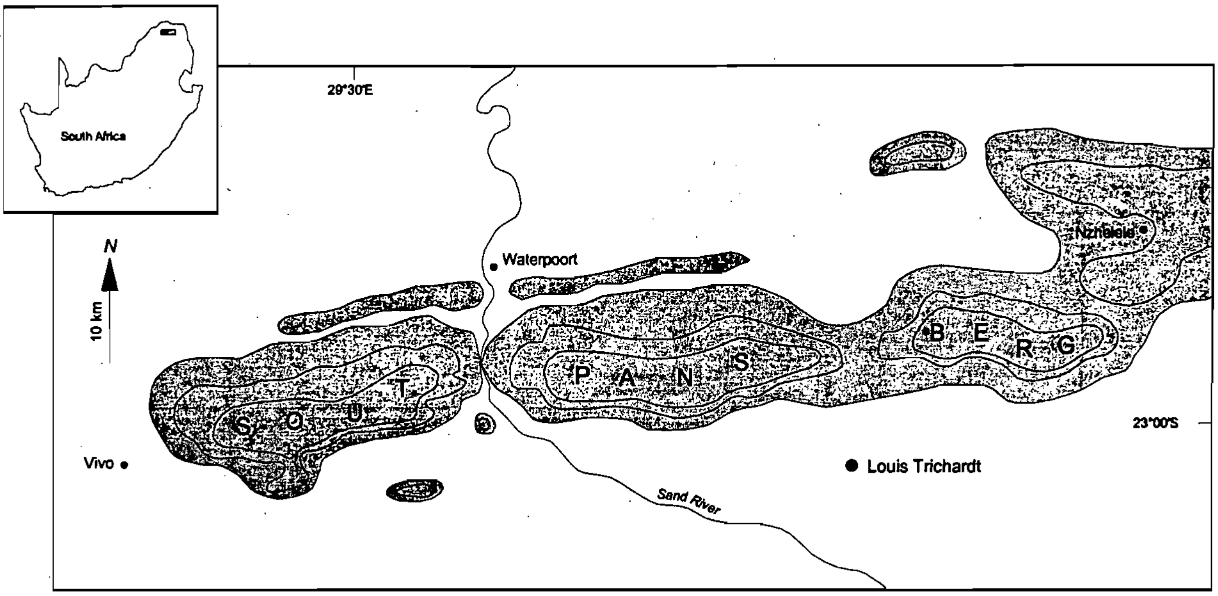


Figure III Location and basic goegraphy of the Soutpansberg study area. Shading denotes areas of high relief.

ideas concisely, while maintaining a logical flow between chapters. Some repetition of information was considered necessary to establish each chapter as a self-contained whole. The general outline of the thesis is as follows: Chapters 1 & 2 quantify differences in the macro and microhabitat affinities of Peregrines and Lanners in South Africa, and the consequences of these differences in terms of distribution and abundance. Chapter 3 examines morphological differences between the two species and the implications of these differences in terms of flight performance, energetics and foraging mode. Chapter 4 investigates the relationship between Peregrine foraging efficiency and the physical structure of the environment. Chapter 5 presents diet analyses for each of the study populations, quantifies differences in dietary niche width, and measures or infers differences in foraging habits and habitats. Chapter 6 compares and contrasts the quality of parental care observed at active nests as an index of habitat quality. Chapter 7 establishes correlates of breeding success of Peregrines and Lanners in South Africa. Chapter 8 synthesizes the most significant results of the study, assessing the relative importance of resources and competition in limiting Peregrine populations in South Africa. There is also an extrapolation of these results into a general commentary on large falcon distribution and the link between latitude, food supply and success in specialized predators.

Study areas and general methods

Because the 'broadest features of the ecology of these two falcons' (Cade 1960) had already been documented, I opted for an intensive approach, concentrating my efforts on gathering data from three small populations of resident pairs over a number of years. Study areas were selected mainly on the basis of the known distribution of Peregrine nest sites at the start of the study, and within logistical and practical constraints. For purposes of comparison, it was also considered important to gather data from a wide range of latitudes and environments.

Some potentially valuable field techniques, for example radio-telemetry, proved impractical for addressing key questions of the study (see Jenkins & Benn 1998). Others, such as marking individuals to investigate population dynamics, were used with more long-term objectives in mind, and have yet to yield meaningful results.

Information on breeding success was collected over nine seasons, from 1989–1997. Other aspects of the study were completed well within this period, using data from fewer years. The number of known falcon territories in each study area tended to increase as the study progressed, either as previously unknown areas were searched or as new pairs became established.

Cape Peninsula

Up to 17 pairs of Peregrines (Appendix 9) were observed and monitored on the Cape Peninsula, Western Cape Province (about 34°10'S, 18°25'E). I lived in this area throughout the study period and made regular visits to many of the Peregrine sites throughout the year. The study area of about 1350 km^2 included Table Mountain, the Tygerberg Hills to the northeast, and the peninsula mountain chain south to Cape Point (Fig. I). The peninsula itself comprises a central, discontinuous range of mountains and steep, rocky ridges extending southwards from Table Mountain. The suburbs of Cape Town extend along the east and west sides of Table Mountain, and sprawl across the Cape Flats to the southeast (Fig. I). The east coast is built up from Muizenberg south to Simonstown, the west coast has an urban centre at Hout Bay and settlements at Kommetjie and Scarborough, and a band of suburban development connects Fish Hoek on the east coast with Noordhoek on the west. Peregrine pairs were resident on montane or marine cliffs around the periphery of the mountain chain, and on buildings and in quarries on the flats.

The area is situated in the Cape Floristic Region of the Fynbos biome (Low & Rebelo 1996). The natural vegetation is typically low, species-rich heathland, comprising varying proportions of woody Proteaceae, grassy Restionaceae and ericacious heaths. Mountain Fynbos covers most of the higher-lying areas and Sand Plain Fynbos occurs on the flats, with patches of Afromontane Forest on the protected eastern slopes of the mountains, and Dune Thicket along the coast (Cowling *et al.* 1996, Low & Rebelo 1996). The spread of invasive alien vegetation (mostly pines, eucalypts and acacias) and urban development has modified many of these habitats. Altitude ranges from sea level to about 1100 m. This climate is temperate. Annual rainfall varies locally from about 400–2000 mm, and falls mostly during winter (May to September) (Cowling *et al.*, 1996). Temperature ranges from an average winter minimum of about 9°C to an average summer maximum of about 25°C. The area is windy, with strong southeasterlies (25–50 km h^{-1}) prevailing in summer, and northwesterly gales (20–40 km h^{-1}) in winter (also see Appendix 11).

Orange River

Up to eight pairs of Peregrines were monitored annually on the lower Orange River, Northern Cape Province (about 28°30'S, 17°00'–20°40'E) (Fig. II). Although most sections of about 500 km of the river from Kakamas west to Sendelingsdrif were surveyed at some time during the study, Peregrine sites were located only at the Augrabies Falls National Park (two pairs), 320 km downstream in the vicinity of Vioolsdrif (five pairs), and a further 160 km downstream on the western edge of the Richtersveld (one pair) (Fig II). The Augrabies sites were within a narrow, sheer-sided gorge which extends downriver from the Augrabies Falls, while the western sites were were on bluffs or escarpments overlooking the river. Flight and foraging data were collected at two Lanner sites at Augrabies over a short study period in 1994 (Chapter 3).

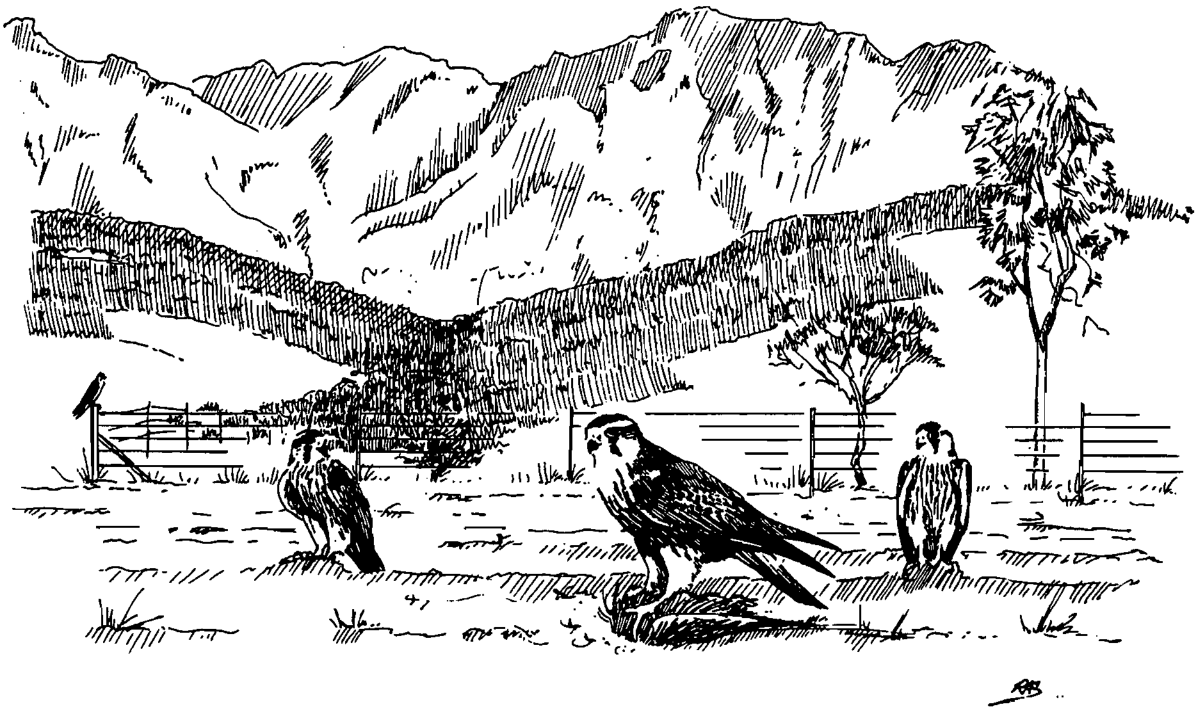
This is an arid, hilly to mountainous area which straddles the Nama (east) and Succulent (west) Karoo Biomes. Vegetation is termed Orange River Nama Karoo from the east as far downstream as Vioolsdrif, Upland Succulent Karoo in the eastern and central Richtersveld, and Lowland Succulent Karoo west of Sendelingsdrif (Low & Rebelo 1996). Throughout, the terrain is rocky and broken and ground cover is sparse except for narrow strips of riparian bush or irrigated croplands along the banks of the river. Altitude varies from about 30–700 m above sea-level and the climate is hot and dry. Rainfall averages about 60–130 mm per annum, and falls mostly in summer in the east and in winter in the west. Temperatures range from a mean winter minimum of about 4°C to a mean summer maximum of about 38°C. Winds are generally light in the east of this region, but strong north- or southeasterlies (up to 40–50 km h^{-1}) may blow in the west, particularly in summer (also see Appendix 11).

Soutpansberg

Up to seven Peregrine nest sites were monitored in the Soutpansberg range, Northern Province (about 23°00'S, 29°40'E), and an intensive study comparing the breeding biology of these birds with a sympatric population of nine pairs of Lanners was conducted from 1991–93. The study area included about 80 km of the south-facing Soutpansberg escarpment, just north of Louis Trichardt, from Nzhelele west to Vivo (Fig. III).

Falling just within the tropics (Fig. III), this is essentially a woodland area, and features moist Sour Lowveld Bushveld, Mixed Bushveld and Afromontane Forest on the eastern slopes, and drier Soutpansberg Arid Mountain Bushveld along the range to the west and north (Low & Rebelo 1996). Patches of grassland and protea woodland occur along the summit of the mountain (Tarboton 1990), which descends northwards gradually to an arid savanna plain. Forestry plantations and subtropical fruit orchards cover much of the upper, eastern parts, while cultivated fields, heavily grazed savanna and rural settlements extend over the flats to the south. Altitude ranges from about 900 m at the foot of the mountains to 1700 m at the highest point. Daily temperatures range from a mean winter minimum of about 5°C to a mean summer maximum of about 30°C. There is low to moderate summer rainfall (about 400–1000 mm per annum), increasing on a gradient from northwest to southeast (Tarboton 1990). Winds are generally light northeasterly (up to 10–15 km h^{-1}) (also see Appendix 11).

Data were collected opportunistically from a number of additional areas around the country, including the Mpumalanga Drakensberg escarpment, the KwaZulu-Natal midlands, the highlands of Lesotho and parts of the Eastern Cape Province (see Chapter 2).



Chapter One

The influence of habitat on the distribution and abundance of Peregrines and Lanners in South Africa

"The Peregrine and the Lanner may be both found in many parts of Africa, but it is the Lanner that is the characteristic, successful, and common species; the Peregrine is normally rare." (Leslie Brown, African birds of prey, *Collins 1970)*

***Summary** – The distribution of Peregrines and Lanners in South Africa was compared using recorded sightings from various sources, including the Southern African Bird Atlas Project. Falcon distributions (expressed as simple, presence/absence ranges and in terms of reporting rates) were overlaid on cliff and vegetation distributions to quantify differences in broad-scale habitat use in the breeding and non-breeding seasons. Lanners outnumbered Peregrines in most areas by at least 10:1, and were more widely distributed. Peregrines were more habitat specific than Lanners, in terms of both topographic and biotic requirements. Peregrines were largely restricted to areas with high cliffs throughout the year and there was little to suggest seasonal movements within the population. Peregrines were most frequent in the Fynbos biome in the southwest, and in the woodland biome. Lanners were less dependent on high cliffs, although cliff availability was important in defining the ranges of both species. Lanners were most common in sour grasslands in the east of the country in the breeding season, with possible movements in the non-breeding season into the fynbos and the central, arid Nama Karoo and southern Kalahari. Overall, Peregrines favoured relatively closed habitats and Lanners favoured relatively open habitats.*

Introduction

Descriptive accounts of the status of Peregrines and Lanners in South Africa generally refer to the Lanner as relatively common and to the Peregrine as rare (*e.g.* Steyn 1982, Maclean 1993). Quantitative data suggest that Lanners outnumber Peregrines by between 10 and 30:1 (Brooke 1984 for South Africa, Tarboton & Allan 1984 for the former Transvaal). Only in parts of the Western Province (Pepler *et al.* 1991, Pepler & Martin 1992) and on the Mpumalanga escarpment (Tarboton & Allan 1984) are Peregrines known to be relatively common, even outnumbering Lanners in some areas (*e.g.* the Cape Peninsula – Hockey *et al.* 1989, pers. obs).

Raptor populations are limited by two primary resources: food and nest sites (Newton 1979). The basic food and nest site requirements of Peregrines and Lanners are similar (Cade 1982, Steyn 1982), so the apparently extreme differences in their respective distributions in South Africa (and in most areas of the

Afrotropics – Brown *et al.* 1982) are surprising. It has been suggested that Peregrines in South Africa are limited by a high degree of habitat specificity (Tarboton 1984, Thomson 1984, Jenkins 1988, 1991, Mendelsohn 1988). This chapter presents a broad-scale quantitative comparison of the distribution and frequency of Peregrine and Lanner sightings in South Africa, in relation to the distribution of cliffs, which may influence nest site availability (Jenkins 1991, Thomson 1984, Tarboton & Allan 1984), and vegetation types, which may influence prey availability (Hustler 1983, Thomson 1984, Tarboton & Allan 1984). Because many falcon species are known to undertake local or long-distance migrations in the non-breeding season (Cade 1982), with associated changes in habitat use, habitat selection by Peregrines and Lanners is compared in the breeding and the non-breeding seasons.

Methods

South Africa was defined as the Republic of South Africa, excluding oceanic islands but including the kingdoms of Swaziland and Lesotho. Falcon, cliff and vegetation distribution maps were plotted on a quarter-degree square grid (15' x 15', $n = 1959$ squares).

Cliff availability (Fig. 1.1) was estimated by inspecting the contour spacing on 1:250 000 topographic maps (contour interval 50 m), and subjectively classifying each quarter-degree square into one of three categories. Squares with relatively low topographic relief and no confluent contour lines were considered to have no cliffs higher than 50 m (no cliffs). Squares with moderate topographic relief and at least one confluence of two contour lines were considered to have at least one cliff of between 50–100 m high (low cliffs). Squares with high overall topographic relief and at least one confluence of three or more contour lines were considered to have at least one cliff higher than 100 m (high cliffs).

The map of vegetation types was adapted from one compiled by the Southern African Bird Atlas Project (SABAP, Harrison *et al.* 1997). This divides the area into five biomes, comprising 12 vegetation types, according to the relative proportion of each vegetation type present in each quarter-degree square. Only those squares with a dominant vegetation type (*i.e.* one covering more than 50% of the square) were included in the analysis ($n = 1795$ squares). The biomes and their component vegetation types are the Karoo biome, comprising the succulent, Nama and grassy Karoo, the Kalahari biome, comprising the central and northern Kalahari, the woodland biome, comprising arid, mesic and Mopane woodland, the grassland biome, made up of sweet, mixed and sour grassland (and including patches of coastal and montane forest), and the fynbos biome.

A contingecy table was constructed to assess the overall distribution of cliffs relative to vegetation types (using a χ^2 test), and to compare the relative availability of cliffs in each vegetation type, by generating and comparing adjusted residuals (Everitt 1977) (Table 1.1).

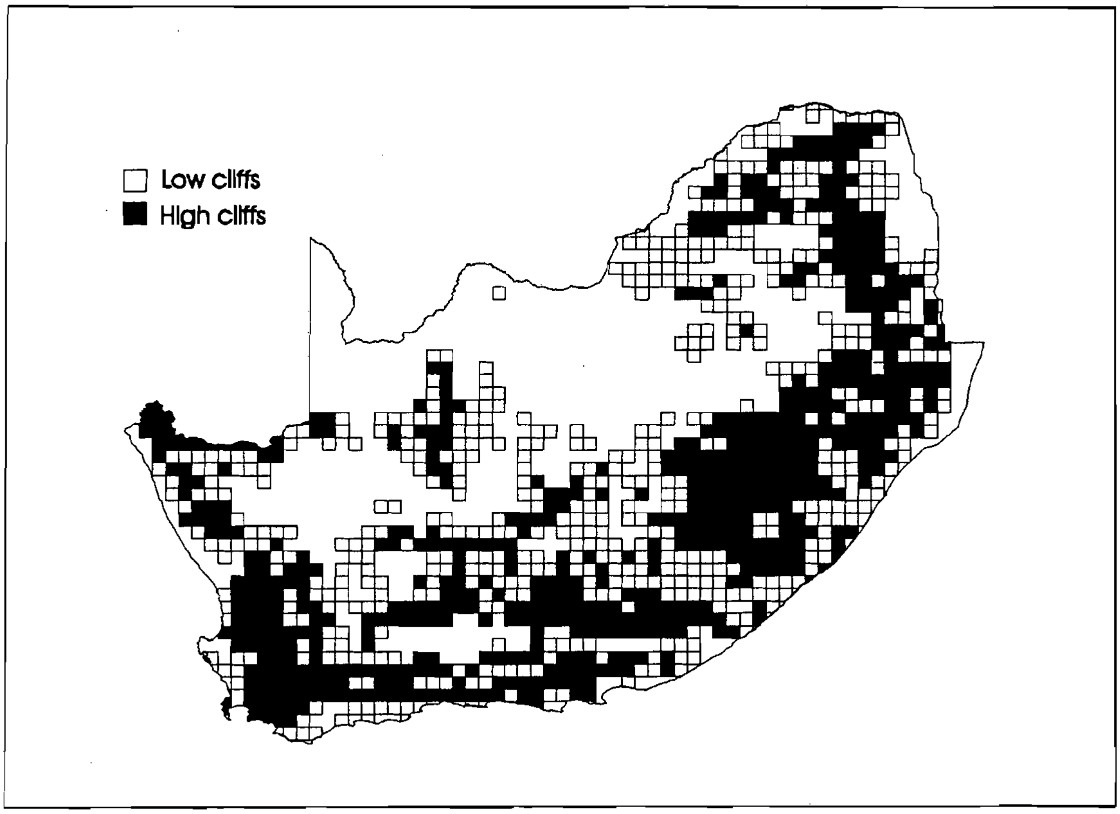


Figure 1.1 The distribution of cliffs in South Africa, plotted on a quarter-degree square grid.

Table 1.1 The distribution of cliffs in relation to the distribution of biomes[a] and their component vegetation types[b] in South Africa

biome	vegetation type	Tot. SQ's[c]	P_t[d]	Obs. SQ's[e]	P_c[f]	Exp. SQ's[g]	residuals[h]
	Succulent Karoo	162	0.090	118	0.115	92	4.3***
	Nama Karoo	343	0.191	170	0.166	196	-3.1**
	Grassy Karoo	110	0.061	76	0.074	62	2.6**
KAROO		615	0.343	364	0.355	351	1.3
	Central Kalahari	153	0.085	25	0.024	87	-10.6***
	Southern Kalahari	85	0.047	13	0.013	48	-8.0***
KALAHARI		238	0.133	38	0.037	136	-13.7***
	Arid Woodland	65	0.036	28	0.027	37	-2.3*
	Mesic Woodland	211	0.118	168	0.164	121	7.1***
	Mopane Woodland	29	0.016	9	0.009	16	-2.9*
WOODLAND		305	0.170	205	0.200	174	3.9***
	Sweet Grassland	94	0.053	29	0.028	54	-5.3***
	Mixed Grassland	179	0.100	119	0.116	102	2.7**
	Sour Grassland	247	0.138	174	0.170	141	4.6***
GRASSLAND		520	0.290	322	0.314	297	2.7***
FYNBOS		117	0.065	95	0.093	67	5.5***

[a] χ^2_5 value for complete set of observed frequencies from contingency table analysis of cliffs relative to biomes = 219.9, $P<0.001$

[b] χ^2_{12} value for complete set of observed frequencies from contingency table analysis of cliff relative to vegetation types = 351.9, $P<0.0001$

[c] Total number of 1/4° squares covered by each biome/vegetation type

[d] Proportion of total number of 1/4° squares covered by each biome/vegetation type

[e] Number of 1/4° squares of each biome/vegetation type with at least one cliff 50 m or more in height

[f] Proportion of total number of 1/4° squares with cliffs in each biome/vegetation type

[g] Number of 1/4° squares with cliffs expected in each biome/vegetation type, if cliffs are distributed in proportion to area of biome/vegetation type

[h] Adjusted residuals of contingency table analysis for each biome/vegetation type (significance: *$P<0.05$, **$P<0.02$, ***$P<0.001$)

Recorded sightings of Peregrines and Lanners were extracted from the published literature, personal communications, personal observations, museum specimen inventories, the Cape Nature Conservation Bird Data Bank and the Southern African Ornithological Society nest record card collection. Combined, these records provide information on where each falcon species has occurred (its range) in South Africa, over the time period they span (from the early 1800's to the present). Except for obviously inaccurate reports, these sightings were accepted and used in the analysis indiscriminately. Such a collation of recorded sightings does not account for variation in the distribution of observers or observer effort, and so cannot be used to determine a species' habitat preferences in terms of relative abundance in different areas. However, an indication of favoured habitats can be obtained by assessing the degree of overlap between bird and habitat distributions.

Peregrine and Lanner sightings from SABAP, from early 1987 to July 1992, were also used in this study. These data can be summarized as reporting rates for a given species in a given area, which express the number of times that species is recorded on bird lists submitted by observers, as a percentage of the number of bird lists received. Hence, the distribution of observer effort is at least partially accounted for and reporting rates may be used as indices of relative abundance, potentially providing greater insight into patterns of habitat use than simple presence/absence analyses (Harrison 1989).

Lanner sightings made between July and November, and Peregrine sightings made between August and December, were classed as breeding season records (Steyn 1982, pers. obs).

The number Peregrine sightings collated in the study was relatively small, so falcon distributions were assessed relative to the distribution of biomes, as well as their component vegetation types. This provided more reliable, but broader scale, information on habitat selection by Peregrines based on larger samples of sightings, and directly comparable information for Lanners. Sightings drawn from the literature and various

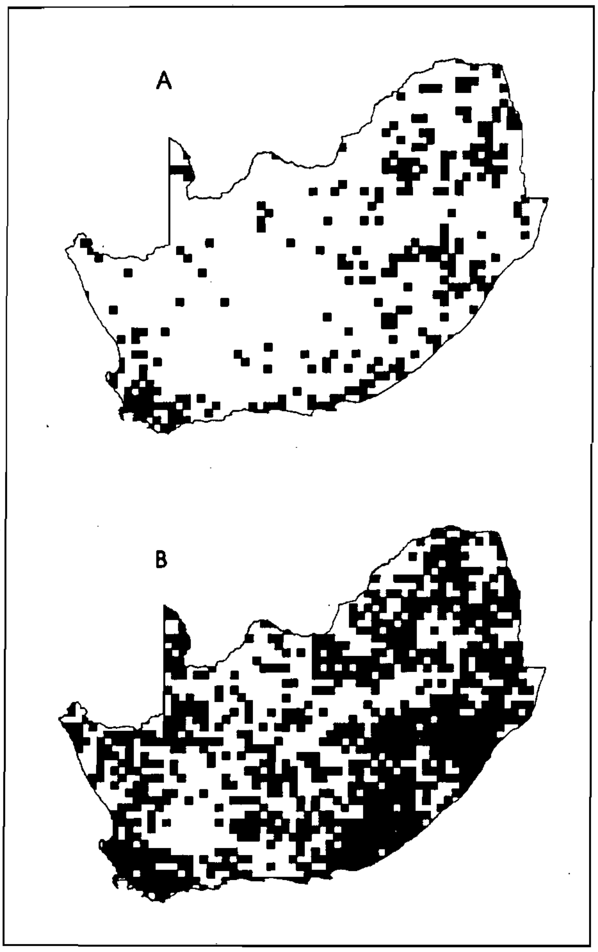


Figure 1.2 The range distribution of Peregrines (A) and Lanners (B) in South Africa, plotted on a quarter-degree square grid. Each shaded square has at least one recorded sighting.

unpublished sources comprised 51% of the total number of Peregrine records available (549 records out of 1077). Therefore it was desirable to use these data in the analysis, rather than simply using the SABAP data with its greater information potential. In contrast, non-SABAP data comprised only 7% of the total sample of Lanner Falcon records (420 out of 5724). In order to make maximum use of the limited data available, and to compare habitat use as adequately as possible, I analysed the data for both species in two ways.

(1) Range *vs* habitat: When the data used in this analysis were extracted, the SABAP coverage for the Republic of South Africa was nearly complete, and comprised over 100 000 field cards, with a minimum of five cards received for almost every quarter-degree square in the country (Harrison 1992). I assumed that by combining this level of coverage with a comprehensive collation of sightings from historical and contemporary South African bird literature, falcons could have been seen and recorded at least once in every square in the country. Using all the available records for each species simple presence/absence range distribution maps were plotted. This minimized, but did not negate, the influence of observer distribution on the distribution of falcon records. Falcon ranges were overlaid on habitat distribution maps, and Jacobs' modification of Ivlev's index of habitat selectivity (*Ei*) (Jacobs 1974) was calculated for each habitat type for each species, in the breeding and non-breeding seasons, where

$$Ei = (p_i - q_i)/(p_i + q_i - 2p_i q_i),$$
$$p_i = N_i/N_t \text{ and } q_i = A_i/A_t,$$

and N_i = number of squares with falcon records in a given habitat, N_t = the total number of squares with

***Table 1.2** Reporting rates of Peregrines and Lanners in the breeding and non-breeding seasons, in relation to the distribution of cliffs in South Africa*

cliff category	breeding		non-breeding		
	NR[a]	RR%[b]	NR	RR%	χ^2;sig.[c]
Peregrines					
no cliffs	30	0.18	45	0.19	0.11
low cliffs	44	0.36	70	0.41	0.51
high cliffs	143	0.98	196	0.99	0.01
Lanners					
no cliffs	521	3.01	1207	5.24	106.76***
low cliffs	531	4.17	821	4.90	8.62*
high cliffs	875	5.95	1349	6.84	10.33**

[a]Number of SABAP records; [b]Reporting rate; [c]χ^2_1 value (with Yates' correction) and level of significance of difference between reporting rates in the breeding and the non-breeding season (*$P<0.05$, **$P<0.005$, ***$P<0.001$)

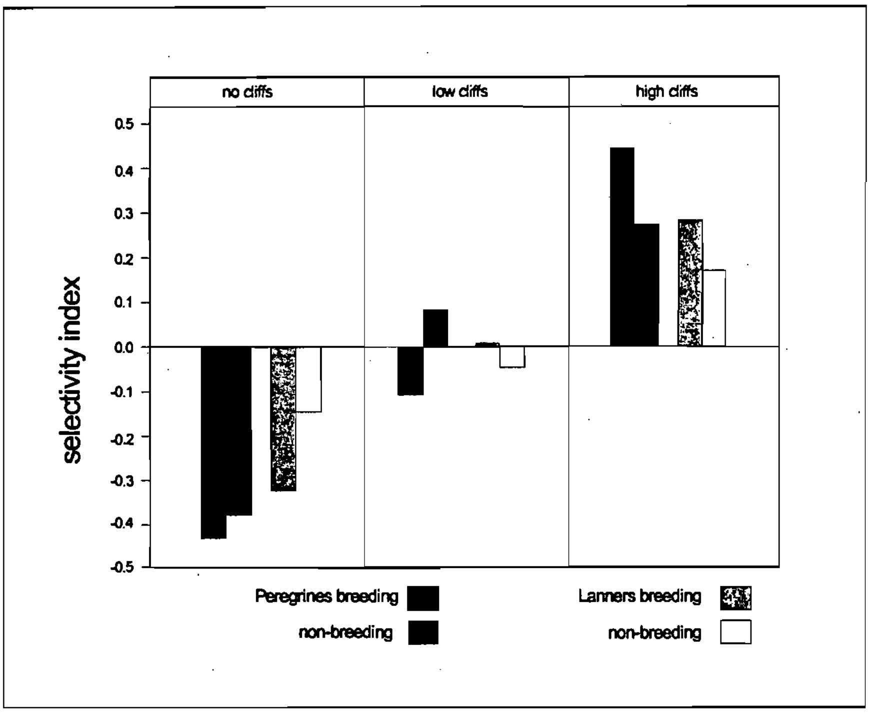


Figure 1.3 Habitat selectivity indices of Peregrines and Lanners in South Africa: bird ranges vs *the distribution of cliffs.*

falcon records in South Africa, A_i = the number of squares making up the given habitat, and A_t = the total number of squares in South Africa. This index can vary from +1 for a strongly preferred habitat to -1 for one which is completely avoided.

(2) Reporting Rates *vs* habitat: Using only the SABAP data I calculated and compared reporting rates for each species over the whole area, and for each habitat type. Reporting rates for each habitat type were calculated in terms of the raw data (rather than as an average of the reporting rates) for each of the relevant squares. This minimized biases associated with spatial and temporal variation in observer skills and observer distribution (Underhill *et al.* 1993). Seasonal changes in reporting rates were tested for statistical significance using χ^2 tests, with the number of atlas cards received for each area in a season defining the 'expected' number of falcon records if habitat use remained constant. The relationship between reporting rate and numerical abundance generally is not linear, and is influenced by the conspicuousness and ease of identification of the target species (Underhill *et al.* 1993). Reporting rates correlate well with other direct measures of abundance in a number of bird species (e.g. Allan 1994), including the Peregrine (Temple & Cary 1990). In this study, differences in reporting rates between habitats and seasons were considered to reflect differences in habitat use. This assumes that Peregrines and Lanners were equally conspicuous in all habitats throughout the year. The comparison is acceptable only because of the general similarity of the two species, which would predict that they are equally identifiable and conspicuous (Harrison 1989).

The suitability of the SABAP database for detecting ecological relationships between bird distributions and environmental variables has been emphasized (Harrison 1992). In this study, the low number of sightings of Peregrines reduced the reliability of the SABAP reporting rates, and required that additional information be used to supplement these data. Additional sightings from various sources provided a more complete picture of Peregrine distribution in South Africa. Neither the range data nor the SABAP data were without sources of bias (particularly with respect to the distribution of observers, confusability of the two species in the field, and differences in the habits of the two species which affect conspicuousness to obervers) and the assumptions listed above probably were not always met. Consequently, the results of the two analyses used must be interpreted with caution, and common elements must be emphasized, while discrepancies must be explained.

Results

A total of 1077 Peregrine sightings were distributed over 301 (15.4%) of the 1959 quarter-degree squares in South Africa (Fig. 1.2), whereas Lanners (5724 sightings) were recorded in 1001 squares (51.0%). The ranges of both species were centred in the eastern and southern parts of the country. Both species occupied larger ranges in the non-breeding season (Peregrines: breeding = 124 squares, non-breeding = 161 squares, Lanners: breeding = 588 squares, non-breeding = 836 squares). However, if allowance is made for the longer duration of the non-breeding season (seven *vs* five months), neither species showed a statistically significant seasonal change in range size (Peregrines: χ^2_1 = 0.36, P >0.75, Lanners: χ^2_1 = 0.072, P >0.75).

The SABAP data yielded an overall average reporting rate for South Africa of 0.51% for Peregrines (n = 528 recorded sightings from a total of over 103 000 atlas cards) and 5.11% for Lanners (n = 5304 sightings). The average reporting rate for Peregrines in the breeding season (0.52%, n = 217) was not significantly different to that recorded for the non-breeding period (0.50%, n = 311, χ^2_1 = 0.19, P >0.05). The average reporting rate for Lanners was significantly higher in the non-breeding season (5.67%, n = 3377) than in the breeding season (4.33%, n = 1927, χ^2_1 = 96.38, P<0.001).

Peregrines favoured high cliff areas and avoided areas without cliffs (Figs 1.2 & 1.3, Table 1.2). The analysis of range *vs* cliff availability suggests that this pattern was less pronounced in the non-breeding season (Fig. 1.3), but this was not supported by the SABAP data (Table 1.2).

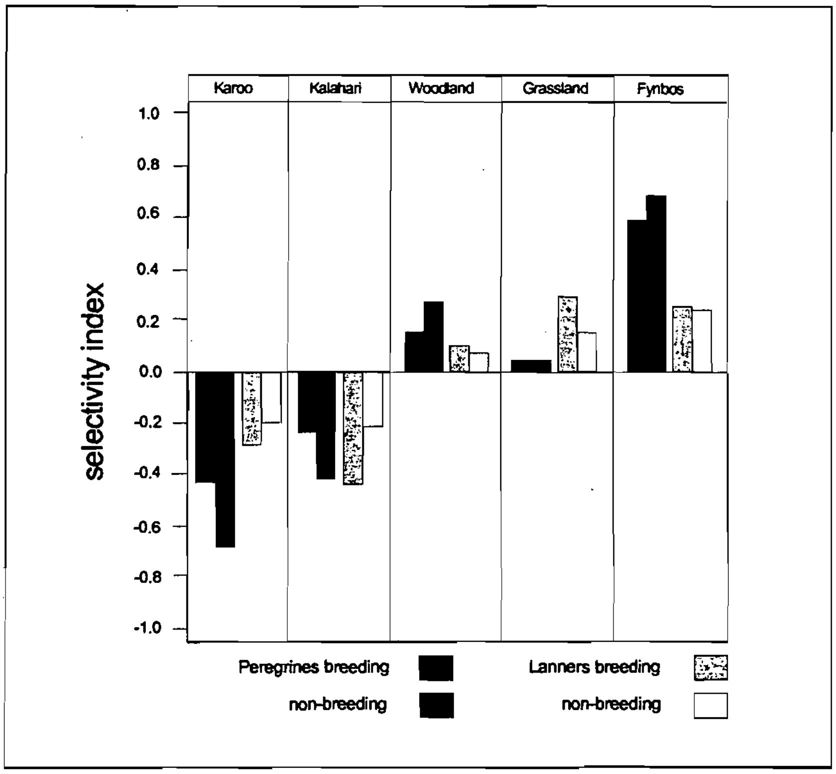
Using only range data, Peregrines seemed to avoid the Karoo and the Kalahari, and were most frequent in woodlands and especially the Fynbos biome (Figs 1.4 & 1.5). In the breeding season, Peregrines occurred most frequently in (mesic) woodlands and the Fynbos, and there seemed to be some movement into arid and Mopane woodlands in the non-breeding season (Figs 1.4 & 1.5). Reporting rates suggested that the relative abundance of Peregrines in the Karoo, the Kalahari and in woodlands was about the same, and that the species was most common in the Fynbos, and rarest in grasslands (Appendix 1). Peregrines were more frequently seen in the succulent Karoo, the Nama Karoo and the southern Kalahari, and less frequently seen in mesic woodlands, than suggested by the analysis of range data alone. There were no significant seasonal changes in Peregrine reporting rates in any of the habitat categories (Table 1.2, Appendix 1).

Lanners favoured high cliff areas over areas without cliffs, but less so than Peregrines, especially in the non-breeding season (Fig. 1.3). Reporting rates increased markedly in cliff-free areas in the non-breeding season (Table 1.2).

Range data indicated that Lanners were generally absent from the Karoo and the Kalahari (especially the central Kalahari), and were most frequent in mesic woodlands, grasslands (especially sour grasslands) and Fynbos (Figs 1.3 & 1.4). This pattern was less defined in the non-breeding season. Reporting rates showed that Lanners were relatively frequent in the Karoo and the Kalahari (Appendix 1), and were concentrated in the Nama Karoo, the southern Kalahari and sour grasslands throughout the year. Lanner Falcon reporting rates were significantly higher in the Karoo (especially the Nama Karoo), the Kalahari (especially the southern Kalahari) and in the Fynbos in the non-breeding season (Appendix 1).

The two analyses produced some complimentary, and some contradictory results. Consistent findings were that both species (but especially Peregrines) favoured areas with cliffs, Peregrines were mostly found in Fynbos and woodlands while Lanners preferred sour grasslands, and Peregrines showed no significant signs of seasonal movements while Lanners apparently moved into flat, open areas without cliffs (especially the Karoo and the southern Kalahari) in the non-breeding season. The two analyses differed most in their interpretation of falcon distributions in the Karoo and the Kalahari. Both these biomes are large and sparsely populated. Published sightings from the Karoo were few, at least partly because of the low number of observers, and this probably influenced the range

Figure 1.4 Habitat selectivity indices of Peregrines and Lanners in South Africa: bird ranges vs *the distribution of biomes.*



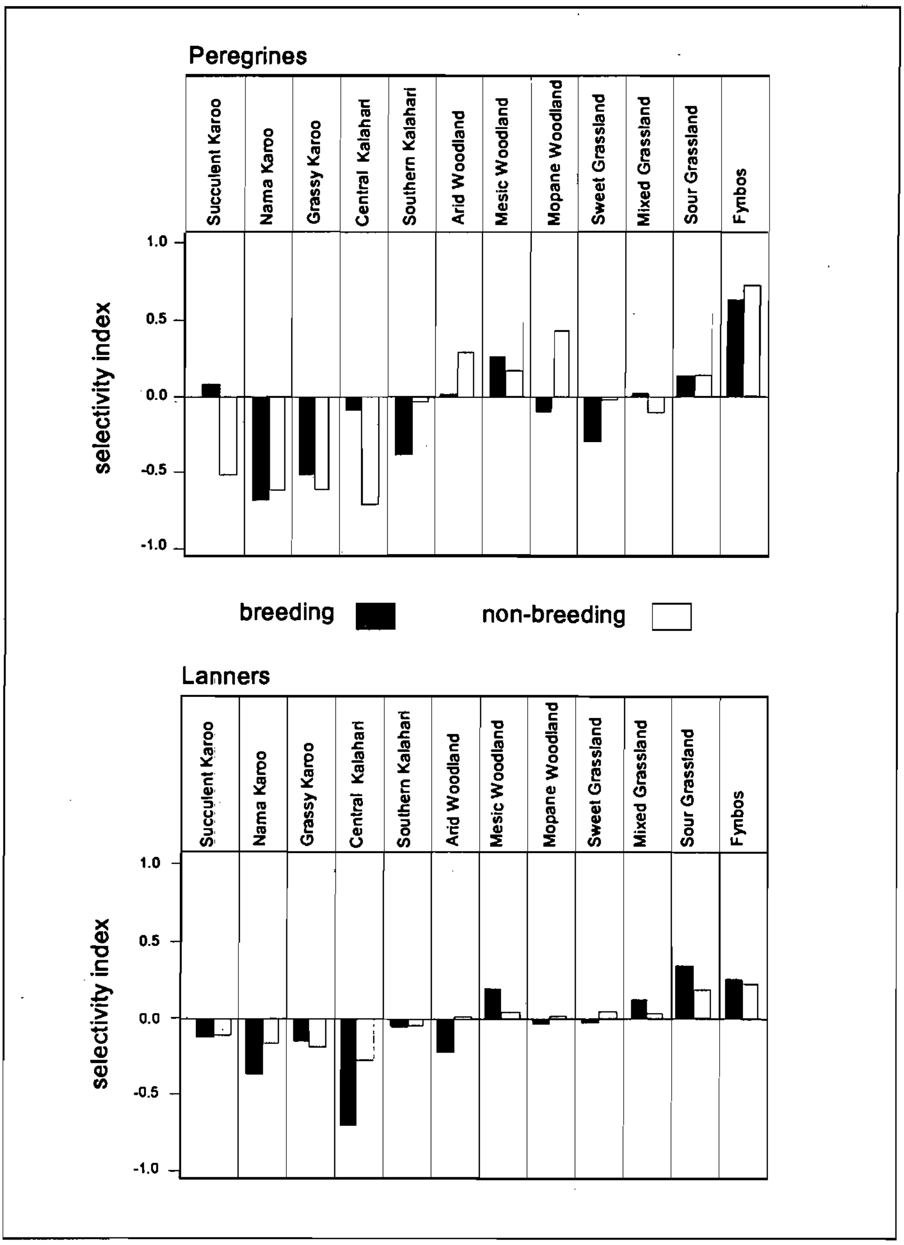


Figure 1.5 Habitat selectivity indices of Peregrines and Lanners in South Africa: bird ranges vs the distribution of vegetation types.

distribution analysis negatively. The Kalahari biome was also poorly sampled, but includes a small area of high coverage (the Kalahari Gemsbok National Park), so falcon ranges were under-estimated in the Kalahari, and relative abundance probably was over-estimated (e.g. the reporting rate of Lanners in the southern Kalahari outside the Kalahari Gemsbok National Park was 9%, compared with 42% inside the reserve).

The distribution of cliffs relative to the distribution of biomes and vegetation types was non-random (Table 1.1). The relative frequency of cliffs was highest in woodlands (especially mesic woodlands), grasslands (especially sour grasslands) and the Fynbos, and lowest in the northern and southern Kalahari and sweet grasslands.

Falcon selectivity indices for vegetation types in the breeding season (Table 1.1, Fig. 1.4) correlated significantly with the relative availability of cliffs in each vegetation type (Spearman's rank correlation coefficient for Peregrines $r_s = 0.71$, $n = 12$, $P<0.01$, and for Lanners $r_s = 0.65$, $P<0.02$), but reporting rates did not ($r_s = 0.150$, $P > 0.5$ and 0.133, $P > 0.5$ respectively) (Table 1.1, Appendix 1).

Discussion

Range size and relative abundance

In the breeding season, Peregrines were restricted to a maximum of six percent of the total area of South Africa, a figure comparable to that suggested by Mendelsohn (1988) for the species over the entire area of the

Afrotropics. Lanners were found over 30% of the the country's area in the breeding season, and therefore occupied a breeding range five times larger than that of the Peregrine.

In terms of the total number of recorded sightings of each species, Lanners outnumbered Peregrines by five to one. The SABAP data, which probably provide more reliable indices of relative abundance, show that Lanners were observed about 15 times more frequently than Peregrines. These measures of abundance may have been influenced by behavioural differences which affect conspicuousness to the observer. For example, Peregrines are relatively sedentary at their nest cliffs (Steyn 1982, Jenkins 1987, Chapters 3 & 4), and therefore may be less readily seen than Lanners by casual observers. Recent surveys by experienced observers in the southwestern Cape (Pepler *et al.* 1991) and in Zimbabwe (Hartley 1992) have shown that in some areas at least, African Peregrines have been overlooked and are more common than was previously thought.

Brooke (1984) suggests that the summer influx to Africa of the migratory *F. p. calidus* could confuse an assessment of the distribution of *F. p. minor*, because the two subspecies are difficult to distinguish in the field. However, the SABAP reporting rate for the Peregrine was not significantly higher from October to March (0.53%, $n = 273$), the period during which *F.p. calidus* is most likely to be present (Dementiev & Gladkov 1966), than for the rest of the year (0.48%, $n = 255$, $\chi^2_1 = 1.28$, $P > 0.10$). This suggests that the migrants probably are not present in sufficient numbers to distort an analysis of the distribution of resident birds.

Seasonal movements

The data presented here indicate that there are no significant seasonal movements by Peregrines in South Africa (Table 1.2, Appendix 1). This is supported by observations in three, widely separated study areas in South Africa, comprising 27 breeding pairs of Peregrines, where pairs remain at their breeding cliffs throughout the year (pers. obs). If seasonal movements do occur within the population they probably involve non-breeding individuals only.

Lanners showed a defined movement into areas without cliffs in the non-breeding season, in terms of both range extensions and changes in relative abundance (Figs 1.3–1.5). Lanners have long been suspected of intra-African migration (Brown 1970, Steyn 1982, Liversidge 1989), and evidence for movements in South Africa has recently been presented (van Zyl *et al.* 1994). In the present study it was not possible to separate movements within the local population from immigration of birds from elsewhere. Significant increases in reporting rates of Lanners in the Nama Karoo and the southern Kalahari in the non-breeding season were not matched by equivalent decreases in reporting rates in other areas of South Africa, and so may indicate migratory influxes from the north (e.g. Herremans & Herremens-Tonnoeyr 1996).

Habitat selection

Higher selectivity indices (Figs 3–5), and relatively greater differences in reporting rates between habitat types (Table 1.2, Appendix 1), suggest that Peregrines in South Africa are more habitat selective, in terms of a broad-scale analysis, than sympatric Lanners.

Differences in the degree to which Peregrines and Lanners favour high cliff areas (Table 1.2, Fig. 1.3) agree with local, quantified differences in nest site selection by the two species, (Tarboton & Allan 1984, Brown & Cooper 1987, Chapter 2), and general statements in the literature (Steyn 1982, Thomson 1984). Previous authors (Thomson 1984, Hustler 1983, Hartley 1992) have proposed an association between Peregrines and woodlands in the Afrotropics. This association is suggested by distribution data from other parts of Africa (*e.g.* Zimbabwe, Kenya), which feature different kinds of woodlands to those present in South Africa, and is only partly supported by the results of this study.

Overall, Lanners tended to favour drier and more open habitats in the breeding season, notably sour grasslands (Appendix 1), and were least common in the Fynbos. In contrast, Peregrines preferred habitats with some form of raised canopy (Fynbos and woodlands), and were rarest in grasslands (Appendix 1). This lends some support to the the suggestion that differences in the hunting methods of the two species influence habitat selection and distribution, and that they may replace each other in different habitats (Tarboton 1984, Thomson 1984).

Correlation between the relative frequency of cliffs in vegetation types, and falcon selectivity indices for vegetation types suggests that cliffs were the most important habitat parameter influencing falcon distributions. However, falcon reporting rates over the range of vegetation types did not correlate with cliff availability, suggesting that the relative abundance of both species, inside their respective ranges, may have been influenced by vegetation type.

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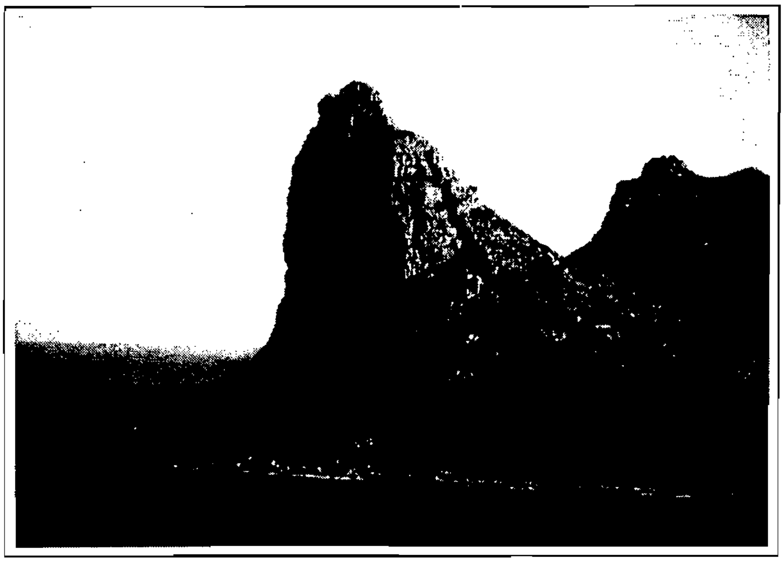

Chapter Two

Characteristics of Peregrine and Lanner nesting habitats in South Africa

" I love my house. I love my nest. In all the world, this nest is best." (P.D. Eastman, The best nest, *Collins and Harvill 1968)*

***Summary** – Peregrine and Lanner nesting habitats in South Africa were described in terms of nest ledge, nest cliff and scree slope parameters, and the environmental context of each site. Data were collected in a tropical study area where Peregrines and Lanners occurred in sympatry, from an allopatric south temperate Peregrine population, and opportunistically for both species from other sites throughout the country. Elevation, ledge size, cliff size and vegetation structure accounted for about 80% of the variation in falcon nesting habitats between species or between populations within species. Peregrines used larger nest ledges on higher, more elevated cliffs than Lanners, overlooking more open, structurally complex vegetation. Temperate Peregrines used smaller ledges on lower cliffs than subtropical pairs, overlooking vegetation which provided less refuge for overflying prey. Temperate Peregrines selected nest sites to minimize the negative effects of spring rainfall. Tropical Peregrines may have selected sites to maximize hunting and provisioning efficiency.*

Introduction

Nesting habitat quality may influence breeding success in birds (Skutch 1976, Cody 1985). The physical features of nest sites contribute to the protection of adults and offspring from predators and adverse weather, and foraging conditions close to the nest affect the energy costs of provisioning (Collias & Collias 1984). Populations with very particular nesting habitat requirements may be limited by the availability of suitable nest sites (Newton 1994). This chapter examines the physical structure of Peregrine and Lanner nesting habitats in South Africa, highlighting regional and interspecific differences in nest site requirements which may partly explain quantified differences in distribution and abundance (Chapter 1).

Methods

Variables used to describe nesting habitats

Up to 32 variables were used to detail the physical structure and location of each falcon nesting habitat included in this study (Appendix 2). These parameters were adapted where necessary to accommodate the few nest sites measured which were not on cliffs. In most cases, ledge and cliff parameters were measured directly, but the dimensions of inaccessible nest ledges or very large cliff faces (where accurate measurement was impractical) were estimated by eye.

Assuming that local foraging opportunities may influence nest site selection, and given the perception that the distribution of cover may differentially affect foraging by Peregrines and Lanners (Tarboton & Allan

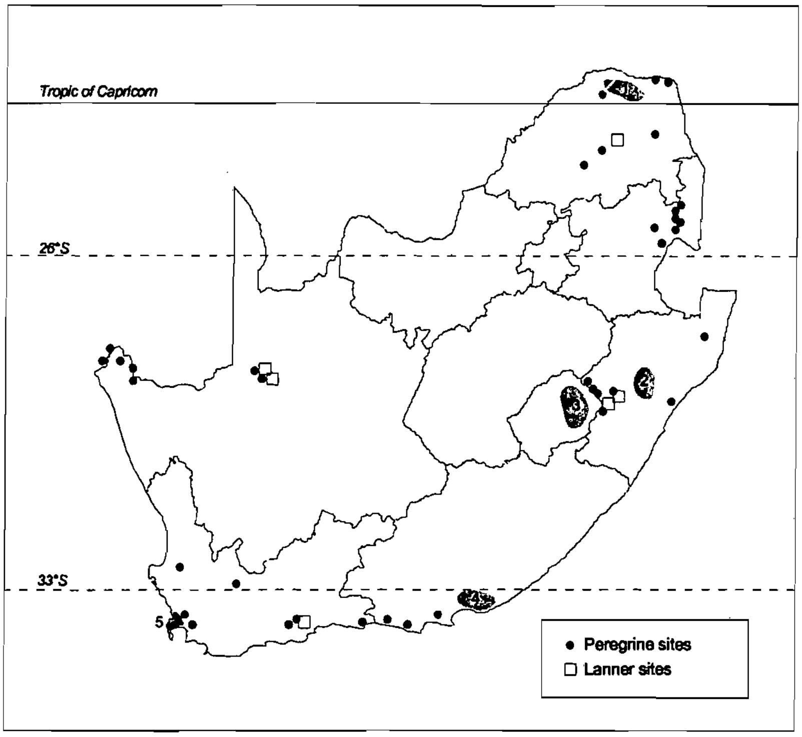

Figure 2.1 Map of South Africa, showing the approximate location of study areas, additional focal populations and other sites where falcon nesting habitat data were collected. Area 1 = Soutpansberg, seven Peregrine sites, nine Lanner sites; Area 2 = KwaZulu-Natal midlands, 24 Lanner sites (data from M. Impey); Area 3 = Lesotho Highlands, 11 Lanner sites; Area 4 = Eastern Cape midlands, 24 Lanner sites (data from A. Stephenson); Area 5 = Cape Peninsula, 13 Peregrine sites.

1984, Thomson 1984), two indices of vegetation structure were measured from 1:5000 aerial photographs of each site. A 20 x 20 cm transparent overlay, marked with a 0.5 cm dot grid of 40 transect lines, was used to estimate the average percentage canopy closure (see Avery 1977) of 1 km^2 of the area overlooked by each nest cliff. A vegetation 'heterogeneity index', reflecting the unevenness of tree and bush distribution, was calculated as the coefficient of variation of canopy closure (Zar 1984). Where canopy closure was less than 50%, standing vegetation was considered as cover for prey from hunting falcons, and the 'prey refuge index' was equivalent to canopy closure. Where canopy closure exceeded 50%, gaps in the canopy were considered as access points for overflying birds to cover below the canopy, and the refuge index was calculated as 100% - canopy closure.

Data collection and analysis

Three data sets were compiled, of varying quality and geographic extent.

Study area nest sites – All active sites in the Soutpansberg and on the Cape Peninsula were measured from 1989–1994. Every occupied nest ledge (and its associated cliff and scree slope) was entered as a separate site. Falcon pairs actively select breeding sites each season from a range of ledges and cliffs available in their territory (Cade 1982, Ratcliffe 1993, pers. obs) so sites used for more than one season contributed proportionally to the total sample. These duplicate data were not strictly independent, but ensured that preferred or frequently used sites were appropriately weighted in the analysis. Meteorological data from the nearest South African Weather Bureau weather station were extracted for each falcon territory in each year to examine the influence of weather on nest site selection. Cliff inventories were compiled for both study areas to provide simple, comparable estimates of nesting habitat available to breeding falcons. These comprise categorial estimates of the aspect, height, length, verticality, face structure and total elevation of every rock face over 10 m high. Eighty-four faces were recorded in the Soutpansberg, with a combined length of about 27 km. One-hundred and sixty-seven cliffs were identified on the Cape Peninsula, totalling about 42 km in length.

All nest sites – A larger sample of complete nesting habitat descriptions from sites in various localities (including the two study areas) (Fig. 2.1) was accumulated opportunistically from 1989–1994. In this data set, each new nest ledge was considered as a separate site but re-used sites contributed to the sample only once.

All cliffs – This sample comprised only basic nest cliff and scree slope measurements and was compiled for all the occupied cliffs visited during the study period, combined with data from other observers for sites I was unable to visit (Fig. 2.1).

In both of the latter samples, Peregrine sites were separated into northern, subtropical sites (those north of 26°S) and southern, temperate sites (those south of 33°S) (Fig. 2.1). Practical constraints limited observer effort to areas where falcon nests were most likely to be found. Overall, 98 complete or partial nesting habitat descriptions were collected from 57 different Peregrine sites, and 87 descriptions were obtained from 76 Lanner sites.

Contingency tables and χ^2 tests were used to identify different frequency distributions in nominal scale data in comparisons of species or area groupings, cliff availability in the two study areas and cliff selection *vs*

Table 2.1 A comparison of cliff habitat available in the Soutpansberg and on the Cape Peninsula, in terms of frequency distributions for six categorial variables. χ^2 goodness of fit tests for significant differences in frequency distributions, and adjusted residuals (in parentheses) identify categories which were relatively more abundant in one area than in the other, *P<0.05, **P<0.01, ***P<0.001

variable	χ^2	study area	abundant categories
cliff height[a]	9.8*	Soutpansberg	2 (2.8***)
		Cape Peninsula	4 (2.0*)
cliff length[b]	52.8***	Soutpansberg	1 (5.0***)
		Cape Peninsula	4 (4.4***)
cliff verticality[c]	6.4*	Soutpansberg	2 (2.5*)
		Cape Peninsula	3 (2.2*)
cliff aspect[d]	84.6***	Soutpansberg	1 (7.1***)
		Cape Peninsula	4 (4.2***)
cliff structure[e]	40.8***	Soutpansberg	3 (5.7***)
		Cape Peninsula	1 (3.7***)
total elevation[f]	21.2***	Soutpansberg	2 (2.6**)
		Cape Peninsula	4 (4.1***)

[a]categories for cliff height (1) >130 m (2) 80–130 m (3) 50–80 m (4) 10–50 m; [b]cliff length (1) >500 m (2) 300–500 m (3) 100–300 m (4) <100 m; [c]cliff verticality (1) overhung (2) vertical (3) slanted; [d]cliff aspect 1–8 sectors of 45°, with increasing exposure to afternoon sun; [e]cliff structure (1) potholes, horizontal and vertical cracks (2) horizontal and vertical cliffs (3) horizontal cracks (4) vertical cracks (5) mostly smooth; [f]total elevation (1) >500 m (2) 400–500 m (3) 200–400 m (4) <200m

availability. Adjusted residuals were generated from contingency tables to identify specific categories where differences were significant (Everitt 1977). Fisher exact tests were used to resolve 2 x 2 contingency tables (Zar 1984). One-way analysis of variance was used to test for significant differences in numerical variables between species or areas. Stepwise discriminant function analysis was used to identify the variables which collectively discriminate between populations. ANOVA and multivariate analyses were done using BMDP software (BMDP Statistical Software, Inc. Los Angeles, California).

Results

Habitat availability and use in the two study areas

The Soutpansberg escarpment features predominantly south and southwest facing cliffs, with a higher frequency of long, vertical, medium-high faces at medium-high elevations than the Cape Peninsula (Table 2.1). Generally, the Soutpansberg cliff-line is fairly uniform in structure, while the Cape Peninsula features a variety of potential falcon breeding sites (including man-made alternatives such as buildings and quarries). Both Peregrines and Lanners favoured the higher, longer cliff faces from the suite of available habitats in the Soutpansberg (Table 2.2), while Peregrines on the Cape Peninsula significantly preferred overhung, medium-low cliffs (Table 2.2). Cape Peninsula Peregrines used significantly more cliffs with easterly aspects (northeast, east, or southeast, 23 used out of 86 available) than westerly aspects (only seven used out of 81 available, χ^2_1 with Yates' correction = 8.54, $P<0.01$), probably to

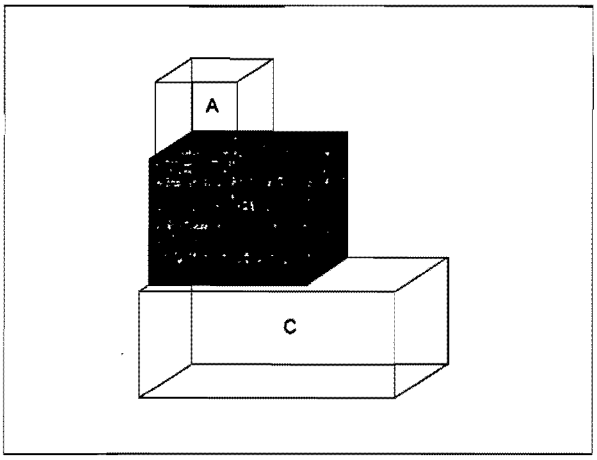

Figure 2.2 Diagrammatic comparison of the dimensions of nest ledges used by (A) Soutpansberg Lanners, (B) Cape Peninsula Peregrines and (C) Soutpansberg Peregrines, based on mean data presented in Appendices 3 & 4.

***Table 2.2** Nesting habitat use* vs *availability by Peregrines and Lanners in the Soutpansberg, and by Peregrines on the Cape Peninsula, in terms of frequency distributions for six categorial variables. Only those variables for which significant results were obtained are shown. χ^2 goodness of fit demonstrates significant differences in frequency distributions, and adjusted residuals (in parentheses) identify relative preference for (+) or avoidance of (-) a specific category,* *P<*0.05,* **P<*0.01,* ***P<*0.001. Categories are defined in Table 2.1 and in Appendix 2*

variable	species	χ^2	categories preferred/avoided
Soutpansberg			
cliff height	Lanner	8.3*	1 (2.4 *)
	Peregrine	9.0*	1 (2.7 *)
cliff length	Lanner	11.6**	1 (3.3 ***); 3 (-2.2 *)
	Peregrine	9.3**	1 (2.9 **); 3 (-2.1 *)
Cape Peninsula			
cliff verticality	Peregrine	21.7***	1 (4.6 ***)
total elevation	Peregrine	12.0**	3 (3.4 ***)

maximize shelter from spring rainfall, which is driven by strong westerly winds in this area.

Regional variation in Peregrine nesting habitats

Study area nest sites – Cape Peninsula Peregrines used shorter nest ledges than Soutpansberg pairs (Fig. 2.2), on smaller, lower, less prominent cliffs overlooking wider valleys and scree slopes with fewer prey refuges (Appendix 3). Discriminant function analysis correctly separated 90% of Peregrine sites into the two study areas according to the length of the scree slope and the area and elevation of the nest cliff (Table 2.3). Relatively more breeding attempts were made in old stick nests (mostly those of Whitenecked Ravens *Corvus albicollis*) on the Cape Peninsula than in the Soutpansberg (7 out of 30 on the Peninsula, 0 out of 22 in the Soutpansberg, Fisher exact test, $P<0.02$).

No significant correlations were found between mean weather conditions in each breeding season and the structure of falcon nesting habitats in the Soutpansberg. On the Cape Peninsula, Peregrines tended to use nest sites protected by wider overhangs in seasons with more rainfall (correlation coefficient $r = 0.71$, $n = 30$, $P<0.001$) and the total exposure of nest ledges was negatively correlated with the number of days with rain in spring ($r = -0.41$, $n = 30$, $P<0.05$).

All nest sites – Peregrines in the subtropical region used sites on shady, south facing cliffs more frequently than south temperate pairs (Appendix 3). Subtropical cliffs were generally larger and more prominent (Fig. 2.3), but often less sheer, and had fewer potential nest ledges (Appendix 3). Temperate sites were less elevated and overlooked shorter scree slopes with fewer prey refuges (Appendix 3, Fig. 2.3). Subtropical sites were situated further from freshwater and human settlements. Sites in these two regions were separated successfully in over 80% of cases in terms of three variables describing the scree slope, the cliff and the nest ledge (Table 2.3). A significantly higher ratio of south temperate sites were in old stick nests (temperate 6 out of 26, subtropical 0 out of 19, Fisher exact test, $P<0.05$).

All cliffs – Subtropical nest cliffs were higher, with longer scree slopes (Fig. 2.3) and were more remote from freshwater and human settlements than south temperate sites (Appendix 3). A greater proportion of temperate sites (5 out of 16) than subtropical sites (2 out of 13) were in stick nests, although this difference was not statistically significant (Fisher exact test, $P = 0.29$).

Peregrine and Lanner nesting habitats

Soutpansberg nest sites – Overall, Peregrines and Lanners used similar nesting habitats in the Soutpansberg. Peregrines were less likely to use covered ledges for breeding than Lanners, and instead used long, wide, horizontal cracks with large floor surface areas (Appendix 4, Fig. 2.2). Peregrines used both overhung and slanted cliffs, but most sites were on vertical faces on outlying sections of the mountain range. Lanners used only sheer faces, mostly on the main escarpment, but some sites were on less prominent cliffs (Appendix 4). Scree slopes at Peregrine sites were shallower, and the distribution and structure of vegetation on the slopes was more varied, with more refuge for prey than at Lanner sites. Only Peregrines used sites in commercial forestry areas, and only Lanner sites overlooked cultivated lands (Appendix 4). Over ninety percent of the sites in this sample were correctly classified to species in terms of characteristics of the nest ledge and the scree slope, most importantly the length of the floor of the ledge and the availability of prey refuges on the slope (Table 2.3). Lanners bred in old stick nests more frequently than Peregrines (9 out of 24 *vs* 0 out of 22 breeding attempts respectively, Fisher exact test, P = 0.001).

All nest sites – Peregrines used larger nest ledges than Lanners. Lanners used vertical and near-vertical cliffs only, while Peregrines used overhung and slanted cliffs as well as vertical faces (Appendix 4). Peregrine sites generally overlooked wider valleys at lower altitudes, and were less frequent in agricultural areas (Appendix 4). In this sample, discriminant analysis successfully distinguished between the two species in only about 60% of cases, in terms of only one variable – the length of the floor of the nest ledge (Table 2.3). Lanners used stick nests as breeding sites more frequently, with eight out of 22 Lanner sites in stick nests, compared with only six out of 52 Peregrine sites (Fisher exact test, P = 0.02).

All cliffs – Peregrine cliffs were generally higher, larger and more prominent than Lanner cliffs (Fig. 2.3), and overlooked longer, higher scree slopes and wider valleys (Appendix 4). Peregrines seemed to be less selective for cliff verticality, but tended to use cliffs with more potential nest ledges than Lanners (Appendix 4). Peregrine cliffs were further from agriculture, and most were in conservation areas, whereas Lanner cliffs were mostly on farmland (Appendix 4). Over 65% of

***Table 2.3** Jackknifed classification matrices from stepwise discriminant function analysis of falcon nesting habitat characteristics. Only those sites with data for all habitat variables were included in the respective samples*

group	% correct	cases classified into group	
study area nest sites		Soutpansberg	Cape Peninsula
Soutpansberg	95.5	1	21
Cape Peninsula	86.7	26	4
TOTAL	90.4	25	27
(Eigenvalue = 2.06; canonical correlation = 0.82; standardized discriminant function coefficients: cliff area = -0.73, length of scree slope = -1.55, total elevation = 1.03)			
all nest sites		subtropical	temperate
subtropical	83.3	15	3
temperate	82.6	4	19
TOTAL	82.9	19	22
(Eigenvalue = 1.25; canonical correlation = 0.75; standardized discriminant function coefficients: width of overhang = 0.51, area of cliff = -0.0002, length of scree = -0.85)			
Soutpansberg nest sites		Peregrines	Lanners
Peregrines	90.9	20	2
Lanners	95.7	1	22
TOTAL	93.3	21	24
(Eigenvalue = 3.81; canonical correlation = 0.89; standardized discriminant function coefficients: length of floor of ledge = 1.36, width of overhang = 0.54, vertical exposure of ledge = 0.47, AS = -1.00, refuge index = 0.92, total elevation = -0.48)			
all nest sites		Peregrines	Lanners
Peregrines	52.1	25	23
Lanners	83.3	3	15
TOTAL	60.6	28	38
(Eigenvalue = 0.13; canonical correlation = 0.33; standardized discriminant function coefficient: length of floor of ledge = 1.00)			
all cliffs		Peregrines	Lanners
Peregrines	52.1	25	23
Lanners	77.3	17	58
TOTAL	67.5	42	81
(Eigenvalue = 0.14; canonical correlation = 0.35; standardized discriminant function coefficient: cliff height = 1.00)			

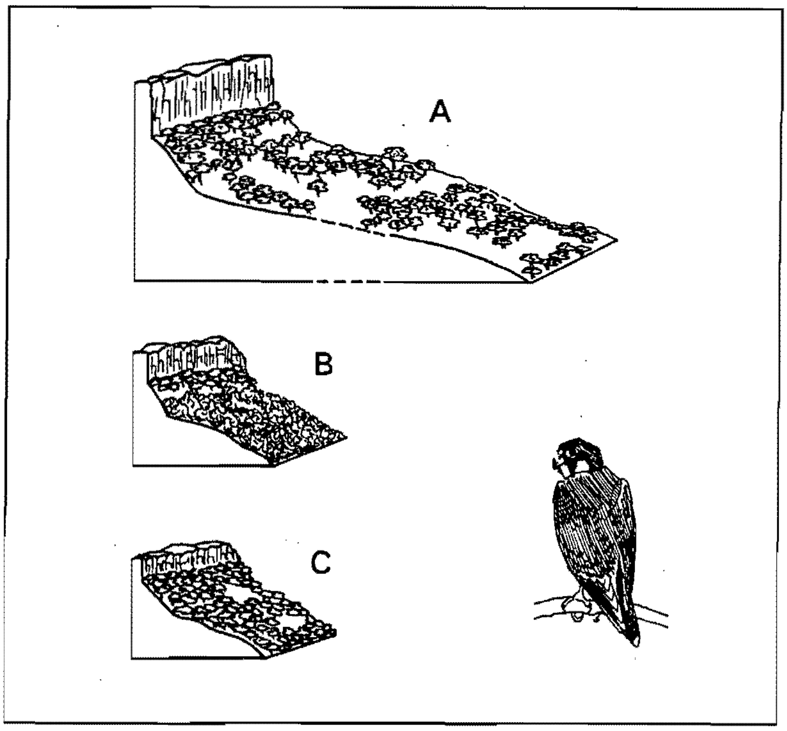

Figure 2.3 Diagrammatic comparison of nest cliff and scree slope parameters of the nesting habitats of (A) subtropical Peregrines, (B) south temperate Peregrines and (C) Lanners in South Africa, based on mean data presented in Appendices 3 & 4.

cases in this sample were correctly classified to species according to one variable, cliff height (Table 2.3). Relatively more Lanner sites than Peregrine sites were in old stick nests, although this difference was not statistically significant (Lanners 21 out of 61, Peregrines 7 out of 39, Fisher exact test, $P = 0.06$).

Discussion

Exposure to climatic extremes

Aspect of falcon nest sites tends to vary with ambient temperature, maximizing insolation in cold climates and minimizing it in warm climates (e.g. Porter & White 1973, Allen 1987, Poole & Bromley 1988). Hence, Peregrines in the northern tropical and subtropical areas of South Africa favoured shady, south facing sites, and generally avoided west facing ledges or cliffs exposed to hot afternoon sun (Appendix 3). Relatively frequent records of Lanners nesting in exposed situations (e.g. stick nests on the top of trees or electricity pylons – Steyn 1982, Kemp 1993), suggest that they are less sensitive to heat extremes while breeding than Peregrines. However, Peregrines on the Orange River were recorded breeding successfully on unprotected, west facing ledges, demonstrating a capacity to endure ambient temperatures in excess of 40°C.

Cold, wet weather reduces breeding success by Peregrines in temperate areas (e.g. Mearns & Newton 1988, Norriss 1995, Olsen & Olsen 1989a, b), and prevailing winds which drive rain fronts affect the orientation of nest sites. Cape Peninsula Peregrines were similarly influenced by poor weather, with breeding pairs favouring sheltered, overhung cliffs and enclosed nest ledges, particularly in years with high spring rainfall.

Use of non-cliff nesting habitats

With the exception of one Lanner site in a corvid nest on an electricity pylon, all of the nests included in this analysis were on cliffs or analogous structures (quarries and buildings). While there are no substantiated records of African Peregrines using tree or pylon sites (Steyn 1982, Mendelsohn 1988), this study has underplayed the Lanner's capacity to breed in alternative situations in areas devoid of cliffs (Steyn 1982, Kemp 1993). Data from the Southern African Ornithological Society nest record card collection are more representative: 81 (72%) of 113 Lanner nest sites were on cliffs, quarries or buildings and 32 (28%) were in stick nests in trees, pylons or on telephone poles. Tarboton & Allan (1984) recorded a similar ratio of cliff:tree or pylon nests in a sample of 157 Lanner sites in the former Transvaal Province.

Two Peregrine sites on the Cape Peninsula were in quarries, and one pair bred on a building in a specially provided nest box. This readiness to use man-made structures was not shown by Peregrines further north in South Africa, although breeding has been recorded in quarries and on buildings elsewhere in the Afrotropics (Steyn 1982, Mendelsohn 1988).

Avian predators and competitors

Other cliff-nesting raptors and ravens may compete with falcons for nest sites (Ratcliffe 1993) or otherwise influence the distribution of breeding pairs (e.g. Poole & Bromley 1988), perhaps because of the threat they pose as predators of eggs and young. Black Eagles *Aquila vereauxii* were quite common in the Soutpansberg (at least seven pairs bred on the cliffs surveyed in the study area), and at least nine pairs of Whitenecked Ravens nested on the Cape Peninsula (pers. obs), but neither species obviously affected nest site choice by Peregrines or Lanners, and falcon pairs bred successfully within 200 m of active eagle and raven nests.

Nest site selection by large falcons may be influenced by the presence of sympatric congeners (White & Cade 1971, Newton 1979, Kemp 1993) and competition for nest sites between Peregrines and Lanners could affect their distributions in southern Africa (Thomson 1984, Tarboton & Allan 1984). Earlier breeding may favour Lanners, which occupy and defend sites before Peregrines and may exclude them from smaller cliffs (Thomson 1984). However, at three points along the Soutpansberg cliff-line, Peregrines and Lanners bred successfully at sites as little as 150 m apart, and in over 500 h of observation at sites in this area, only three aggressive encounters between Peregrines and Lanners were observed (ARJ, unpublished data, S.T. Wagner pers. comm.). Hence there was little to suggest active displacement of one species by the other, or direct competition for nest sites.

The size of the nest ledge

Nest ledge size was an important factor discriminating between falcon populations in this study (Appendices 3 & 4, Table 2.3, Fig. 2.2). The size and shape of the nest ledge affect the thermal microenvironment of the nest (Williams 1984, Boyce 1987), and subtropical Peregrines may have used larger nest ledges than Lanners and south temperate Peregrines to accommodate warmer environmental temperatures while breeding, reducing the risk of hyperthermia in cramped broods (e.g. Lombardo 1994). Alternatively, differences in nestling spatial requirements may be related to differences in food supply. Hunger is likely to increase competitive activity in raptor nestlings (e.g. Newton 1978, Simmons 1986). At nest sites with restricted space, restless and aggressive young may prevent adults from distributing food efficiently (Newton 1978, Hubert *et al.* 1995), and squabbles for food may cause nestlings to fall out of the nest or to vacate it prematurely (e.g. Simmons 1986, Allen 1987). Subtropical Peregrines may have been subject to poor foraging conditions, and used large nest ledges to minimize accidental nestling mortality and maximize provisioning efficiency to hungry broods.

Restriction to large nest ledges apparently prevented subtropical Peregrines from using small, disused stick nests of other cliff-nesting species, especially those of Whitenecked Ravens. These structures were common on cliffs in both study areas, and were used frequently by Peregrines on the Cape Peninsula (23% of breeding attempts) and by Lanners in the Soutpansberg (38% of breeding attempts).

Cliff height and hunting efficiency

While high, vertical cliffs function in protecting falcon nest ledges from terrestrial predators (Mearns & Newton 1988, Ratcliffe 1993), differences in the cliff height requirements of Peregrines and Lanners in South Africa (Appendices 3 & 4, Table 2.3, Fig. 2.3) cannot be explained in terms of differences in predation pressure. In sympatry, the two species face the same range of nest predators and should be afforded equal protection by cliffs of equal size. Greater diversity or abundance of terrestrial predators in the tropics could account for differences in the height of cliffs favoured by subtropical and south temperate Peregrines (Table 2.4). However, Peregrines have been recorded breeding on small, accessible cliffs in other areas of the Afrotropics (Brown 1970, Thomsett 1988, Hartley 1992), and temperate pairs were subject to higher levels of human disturbance (pers. obs), an important factor modifying nesting habitat use by Peregrines in other parts of the world (e.g. Mearns & Newton 1988, Ratcliffe 1993).

High nest cliffs provide vantage points from which perch-hunting falcons can exploit a localized prey base (Tarboton 1984, Runde & Anderson 1986, Brown & Cooper 1987, Newton 1988). In areas where food resources are limited, high cliffs may be a prerequisite for successful breeding (Tarboton 1984, Jenkins 1991). Hence, Peregrines in subtropical South Africa may require higher nest cliffs than temperate conspecifics and sympatric Lanners (Appendices 3 & 4) in order to breed successfully in an environment with an inferior food supply.

Vegetation structure

The distribution of Peregrine and Lanner pairs in the Soutpansberg relative to the structure of the vegetation along the cliff-line (Appendices 3 & 4, Table 2.3, Fig. 2.3) was contrary to established differences in the broad-scale vegetational affinities of the two species (Tarboton & Allan 1984, Thomson 1984, Chapter 1). However, while Lanners were concentrated at the east end of the mountain range, on cliffs overlooking dense woodland, they may have selected nest sites according to their proximity to rural settlements where free-range domestic fowl were available as prey, and irrespective of the nature of the vegetation immediately adjacent to the escarpment.

Low numbers of high flying or commuting birds in the vicinity of the Soutpansberg could explain why Peregrines used cliffs overlooking relatively open habitats. With a low passage rate of transient birds flying over a continuous canopy (with limited refuge opportunities), Peregrines may favour more heterogeneous woodland (with numerous refuges), where resident birds are vulnerable to predation as they cross clearings or breaks in a discontinuous canopy (see Pruett-Jones *et al.* 1981, Hustler 1983, Czechura 1984, Hartley 1992). Lower prey refuge indices at south temperate Peregrine sites than at subtropical sites (Table 2.5) suggest a greater emphasis by temperate pairs on transient, rather than locally resident, prey.

Nesting habitat and the distribution of breeding pairs

Peregrines in subtropical South Africa are at least proximally limited by the availability of suitable nesting habitat, with breeding pairs restricted to landscape features which are rare in the environment (high, elevated cliffs with large, sheltered ledges). Lanners and south temperate Peregrines are less conservative in their nesting habitat requirements, and are more common and less patchily distributed as a result (Chapter 1).

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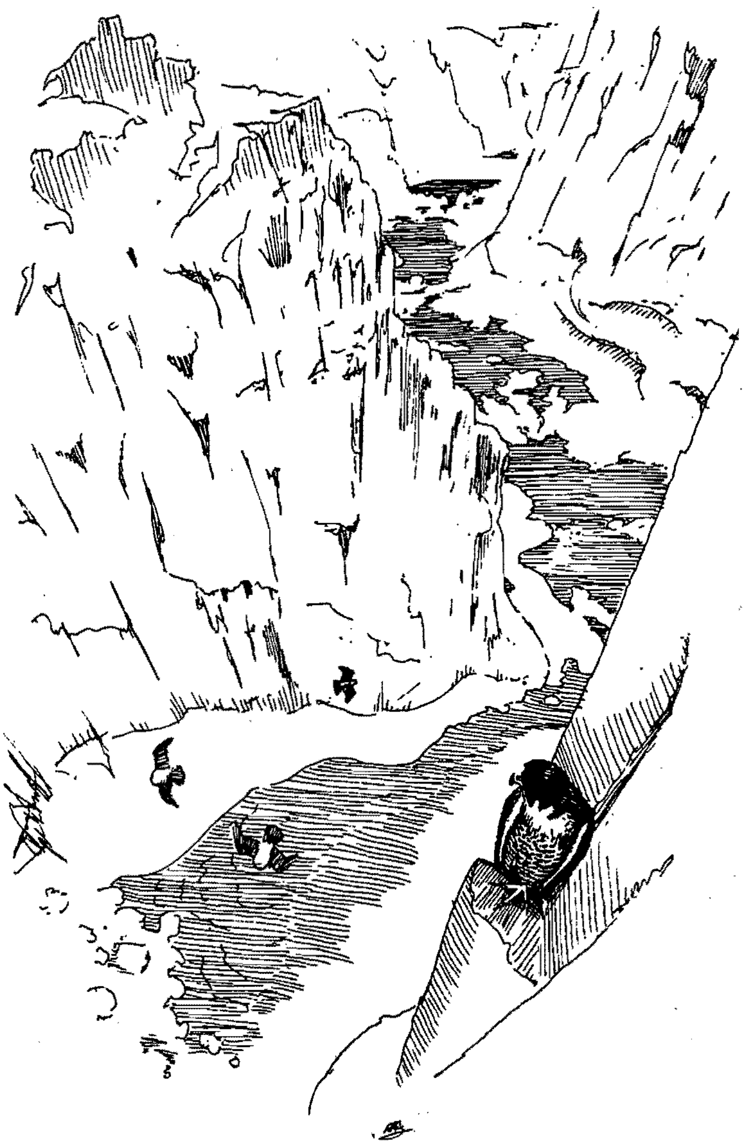

Chapter Three

Morphometrics and flight performance of southern African Peregrines and Lanners

"...as a creature is built for a particular purpose, so its life is held within the limits of its construction."
(William Jordan, Divorce among the gulls, *Abacus 1991)*

Summary *– Twenty-four morphometric parameters were measured from samples of live southern African Peregrines and Lanners. The two species were different in most measurements, especially those relevant to prey capture and handling techniques, and flight performance. Flight performance parameters calculated from mensural data predicted significant differences in the flying abilities of the two species, notably that Peregrines should fly faster in level powered and gliding flight, but incur greater fuel costs in terms of both time and distance flown. Peregrines should glide less efficiently and be restricted in their ability to soar in thermals. Observations of Peregrines and Lanners under uniform environmental conditions largely confirmed these predictions. Peregrines flew faster but for less time, flapped more and soared in thermals less than Lanners. Theoretically, Peregrines should tend more towards sedentary perch-hunting than Lanners, and be more habitat selective as a result. Observations and distributional data from South Africa corroborate this. Form and functional differences in these two falcons may be related to differences in foraging mode, distribution and abundance. Similar inferences may be drawn from morphological comparisons of other large falcons to provide proximate explanations for broad-scale patterns of distribution.*

Introduction

Morphometric data have been used as both evidence for and predictors of differences in flight performance and feeding ecology of co-existing raptors. Intraspecific studies have compared birds of different races (e.g. White 1982), sexes (e.g. Andersson and Norberg 1981) and age classes (e.g. Mueller *et al.* 1981, Brown 1989). Interspecific studies have been concerned mainly with niche partitioning (e.g. Barnard 1986). Authors have tended to emphasize the importance of specific wing and tail parameters in predicting the energetic costs of flight and hence the optimum hunting mode (e.g. Jaksić and Carothers 1985). Other morphometric characters, such as toe and tarsal lengths and bill sizes (Cade 1982, White 1982), are thought to be associated with food handling abilities.

Differences in the feeding ecologies and habitat preferences of southern African Peregrines and Lanners should reflect differences in their respective morphologies and flying and hunting abilities (e.g. Moermond 1990, Norberg 1995). This chapter examines the relationship between form and function and distribution and abundance in these two falcon species.

Methods

Mensural data were used to predict flight performance parameters which might influence foraging mode, food and habitat selectivity, dispersability and ultimately population status. Field observations of hunting and flying behaviour of the two species under the same conditions were then used to test these predictions. Intraspecific differences between adults and immatures were also examined.

Morphometrics

Body mass, wing area, wing loading, aspect ratio and 20 linear parameters were measured from a total of 73 live falcons and one recently dead specimen. The sample comprised 33 Peregrines (15 adult females, five immature females, eight adult males and five immature males) and 41 Lanners (nine adult females, 12 immature females, seven adult males and 13 immature males). Any bird not in full adult plumage was considered immature. Of the birds measured, 14 Peregrines and 28 Lanners were live-trapped in the Transvaal and the Cape Province, South Africa, between 1989 and 1994. The remainder were captive birds from various sources (either injured, in captive breeding facilities or being flown by falconers).

Measurements taken and units used were mostly those of Biggs *et al.* (1977) and Mendelsohn *et al.* (1989) except where they were relevant for flight performance calculations, in which case they followed Pennycuick (1989). Body mass was measured correct to the nearest 10 g, using either a 1000 g or 1500 g spring scale for wild-trapped birds or various balance scales for captive birds. Linear measurements were taken to the nearest 0.1 mm using Vernier calipers or to the nearest 1 mm with a ruler or tape measure. Wing area was measured to the nearest 1 cm^2 from a tracing of the extended wing, flattened dorsally. All flight performance parameters were calculated using the computer programs in Pennycuick (1989). The mass of the crop contents of wild-trapped birds was estimated according to the degree of crop distension (10 g increments from 10 g to 50 g), and subtracted from the measured mass to give an empty mass for all individuals. Ten per cent was added to the actual body mass of falconry birds to approximate wild condition. Morphometric data for each species were grouped by sex. Data for Peregrine females and Lanner males were tested for differences between wild-trapped and captive birds. These two groupings had the most comparable samples of birds from each source. Data for both sexes of both species were tested for differences between adults and immatures.

Predicted flight performance

The body mass, wing span and wing area measurements of each individual were used to calculate flight performance parameters with Pennycuick's (1989) computer Programs 1 and 2. The parameters calculated for horizontal flapping flight were: *minimum power speed* (V_{mp}) – the air speed at which power output for flight is least, *maximum range speed* (V_{mr}) – the air speed at which the ratio of power to speed is lowest, *effective lift:drag ratio* (L/D max) at V_{mr}, *fuel consumption* – grams of fat consumed per km flown at V_{mr}, the minimum aerobic scope – the mimimum power required to fly (P_{min}) divided by an estimate of the basal metabolic rate (P_{met}) (see Pennycuick *et al.* 1994). The parameters calculated for gliding flight were: *stall speed* – the minimum glide air speed required to avoid stalling, *minimum sinking speed* – the lowest rate of descent attainable, *best glide ratio* – the best achievable ratio of forward to downward movement, flying at the best glide speed, the *best glide speed* (V_{bg}) the air speed at which the ratio of power to speed is lowest, *circling radius* – the minimum radius of a thermal in which the bird is able to climb, banking at a standard angle of 24°, and *cross-country speed* (V_{xc} (opt)) – the ground speed of cross country flights if inter-thermal glides are made at optimum speed and using thermals rising at a standard speed of 5 m s^{-1}. For more details on the derivation of these parameters see Pennycuick (1989). The programs' default values for acceleration due to gravity (9.81 m s^{-1} – standard earth gravity) and air density (1.23 kg m^{-3}) were used throughout.

Two-sample Student's *t* tests were used to test the significance of differences between the means of each morphometric variable in each of the groupings compared. For those variables where significant differences were found between adult and immature birds in within-species comparisons, only data for adult birds were used in between-species comparisons to prevent the proportion of immatures from influencing the result.

Observed flight performance

Two adult pairs of each species were observed in the Augrabies Falls National Park (AFNP), South Africa (28°S,20°E) between 25 April and 16 May 1993. The birds are resident in the park, and breed on the walls of a deep gorge along the lower reaches of the Orange River. The gorge is about 15 km long, and features open expanses of sheer and semi-sheer rock on both sides. The cliffs vary from about 80–120 m high, and the valley is about 150–500 m wide. The gorge runs through an area of undulating, rocky hills, at about 650 m above sea level. The area generally is dry, and vegetation is sparse and mostly confined to the watercourses. The nest cliffs of the four pairs of falcons are spaced unevenly along the first 8 km of the gorge, downriver from the falls. Although the gorge is narrower, shallower and steeper-sided at its upper end than its lower end, overall it provides a structurally uniform habitat for foraging falcons, ideally suited to a study comparing the hunting and flying behaviour of the two species.

Peregrines and Lanners do not breed at the same time in southern Africa (Steyn 1982, Chapter 7). This study was conducted in the non-breeding season of both species, and was timed to exclude as much as possible the influences of moult, courtship and breeding on maintenance activity budgets. Falcons were observed using 10 x 40 binoculars and a 20–60x spotting scope, at distances of 100–1500 m. Periods of observation ranged from 1.6 h to 11.5 h. Eighteen observation periods were completed at Peregrine sites and 13 at Lanner sites, totalling 104.3 h and 100.9 h of observation respectively. All bird activities were recorded on a dictaphone, and subsequently were timed correct to the nearest second, and transcribed. Activities were divided into four categories: *perched*, *gliding* (all flying without flapping, including slope soaring in orographic updrafts (Pennycuick 1989) but excluding thermal soaring), *flapping* and *thermaling* (circling and gaining height in a rising pocket of differentially heated air).

A focal bird (Altmann 1974) was selected and its activities were recorded for as long as the bird was in sight, or until the end of the observation period. When one or both of the pair at a site were perched in an easily observable position, it was sometimes possible to record the activities of both birds at once. Observations were made from one or two positions along the gorge wall at each site, and the birds were not actively followed. Data from the two sites for each species were pooled. Times spent on each activity category for each of the observation periods were expressed as percentages of the time birds were in sight, or for flight activities, of the time the birds were observed flying. These percentages were then grouped by species, or within species by weather conditions, and differences were tested for significance using non-parametric Mann-Whitney *U* tests.

Whenever possible, hunts and longer flights were plotted on 1:5000 aerial photographs, using landscape features to estimate the routes followed. These plots were measured and provided indices of strike and flight

Table 3.1 *Morphometric differences between adult and immature southern African Peregrines and Lanners. Sample sizes (adults, immatures): Peregrine males* n = *6, 5; Peregrine females* n = *10–11, 5; Lanner males* n = *7, 13; Lanner females* n = *9, 12. Data given are means ± SD (n.s. = not significant,* *P<0.05, **P<0.01, ***P<0.001)

	adults	immatures	*t* value
Peregrine males			
secondary length (mm)	124 ± 4	137 ± 4	5.43***
outer rectrix length (mm)	132 ± 6	141 ± 4	2.97*
inner rectrix length (mm)	134 ± 7	142 ± 3	2.33*
claw 1 length (mm)	19.2 ± 0.8	18.1 ± 0.7	2.33*
Peregrine females			
secondary length (mm)	149 ± 4	155 ± 4	2.73*
outer rectrix length (mm)	152 ± 5	159 ± 7	2.65*
Lanner males			
outer rectrix length (mm)	159 ± 5	167 ± 7	2.70*
Lanner females			
bill length (mm)	22.3 ± 1.5	21.1 ± 0.9	2.42*
bill width (mm)	16.5 ± 0.7	17.9 ± 1.6	2.38*
claw 2 length (mm)	18.6 ± 1.3	17.3 ± 0.7	2.86**

distances. Indices of strike and flight ground speeds could then be generated in cases where flights were both measured and timed. The observed home range of each of the four pairs was estimated by outlining the minimum area covered by all the flights plotted at each site. When observing bouts of flapping flight, I tried to count the number of beats completed. In flapping bouts longer than 5 s in duration, I divided the number of beats counted by the whole number of seconds elapsed, to result in an index of wingbeat frequency (see Pennycuick 1990). These various indices and estimates are all prone to a substantial degree of error, but this was considered to be equal for both species. The data are intended only to reflect the relative flight performance of the two species. Mean values for flight and strike times, and distance, speed and wingbeat frequency indices were calculated for each species, and for males and females within each species. Differences were tested for statistical significance using Student's *t* tests.

Local maximum temperatures for each day of the study were provided by the South African Weather Bureau. Wind speed was ranked 0–5 (0 = calm, 1 = light, 2 = light to moderate, 3 = moderate, 4 = moderate to strong and 5 = strong) for each observation period.

Results

Morphometrics

No significant differences were found between wild-trapped and captive birds in any of the measurements

Table 3.2 *Flight performance parameters of southern African Peregrines and Lanners, calculated using Programs 1 and 2 from Pennycuick (1989). Data for adults and immatures were pooled, except where these were significantly different, when only adults were compared. Sample sizes: Peregrine males* n = *13, Peregrine females* n = *20, Lanner males* n = *20, Lanner females* n = *21. Data given are means ± SD (n.s. = not significant,* *P<*0.05,* **P<*0.01,* ***P<*0.001)*

	Peregrine males	Lanner males	*t* value	Peregrine females	Lanner females	*t* value
V_{mp} (m s^{-1})	9.1 ± 0.2	8.5 ± 0.2	8.03***	9.8 ± 0.4	9.3 ± 0.3	4.80***
V_{mr} (m s^{-1})	15.0 ± 0.3	14.2 ± 0.3	6.79***	16.2 ± 0.5	15.3 ± 0.5	5.95***
Max. L/D ratio	7.35 ± 0.18	8.12 ± 0.24	9.82***	7.64 ± 0.25	8.28 ± 0.25	8.07***
fat at V_{mr} (g km^{-1})	0.079 ± 0.005	0.068 ± 0.005	5.37***	0.113 ± 0.012	0.098 ± 0.012	3.04**
aerobic scope	15.35 ± 0.84	12.91 ± 0.77	8.61***	17.70 ± 1.30	15.20 ± 1.20	6.58***
stall speed (m s^{-1})	7.62 ± 0.29	6.52 ± 0.29	10.58***	8.02 ± 0.20	7.06 ± 0.30	10.88***
best glide ratio	13.3 ± 0.3	13.9 ± 0.3	5.78***	13.5 ± 0.4	14.0 ± 0.4	3.74***
best glide speed (m s^{-1})	10.2 ± 0.3	9.2 ± 0.3	9.51***	10.9 ± 0.4	10.0 ± 0.4	7.82***
min. sinking speed (m s^{-1})	0.669 ± 0.020	0.578 ± 0.026	9.17***	0.708 ± 0.040	0.627 ± 0.040	6.40***
circling radius (m)	16.7 ± 1.3	12.2 ± 1.1	10.92***	18.4 ± 1.1	14.3 ± 1.3	10.99***
$V_{xc(opt)}$ (m s^{-1})	12.5 ± 0.1	12.2 ± 0.2	5.23***	13.2 ± 0.2	12.9 ± 0.2	4.84***

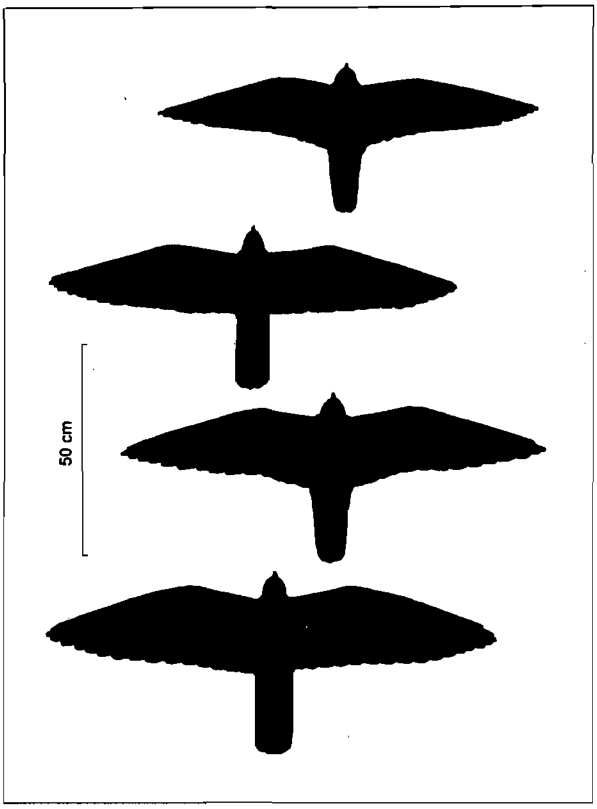

Figure 3.1 Simplified flight outlines of southern African Peregrines and Lanners, based on the morphometric data in Appendix 5.

taken. Immature Peregrines had longer secondary feathers and longer rectrices (only outer feathers in females) than adults in both sexes (Table 3.1), and immature male Lanners had longer outer rectrices than adults. Generally, immatures of both species tended to be lighter and had larger flight surface areas and lower wing loadings than adults, although these differences were not significant. Male Peregrines and female Lanners showed significant differences between adults and immatures in some bill and claw measurments (Table 3.1).

Female Peregrines were significantly different from female Lanners in 18 of the 24 measurements compared (Appendix 5). Bill size, ulna length, tarsus length and aspect ratio were the same. Male Peregrines were significantly different from male Lanners in 17 of the measurements compared (Appendix 5). Body mass, bill size, tarsus length and width, and toe 1 length were the same. Overall, Peregrines tended to be heavier, with longer bills (not significant), shorter bodies, smaller wings, shorter tails and bigger feet than Lanners (Figs 3.1 & 3.2), and had heavier wing loadings and higher aspect ratios.

Predicted flight performance

Pennycuick (1989) recommends that information generated by his programs be compared in terms of percentage change rather than absolute values. In this study, Peregrines and Lanners were significantly different in all the flight performance parameters compared (Table 3.2). These differences predicted that in horizontal flapping flight (i) the speeds at which flight is least strenuous (in terms of fuel consumed per unit time – V_{mp}) and the speed at which the power to speed ratio is lowest (i.e. fuel consumption per unit distance flown is minimized – V_{mr}) (Pennycuick 1989) are 3–5% higher for Peregrines than for Lanners, (ii) the effective lift:drag ratios for flight at V_{mr} are 3–7% lower for Peregrines than for Lanners, (iii) Fuel consumption (grams of fat consumed per km flown at V_{mr}) is 8–9% higher for Peregrines than for Lanners and (iv) the minimum aerobic scope required is 12–15% greater. In gliding flight (i) Peregrines must fly 11–15% faster than Lanners to avoid stalling, (ii) Peregrines achieve a 3–5% lower best glide ratio at a best glide speed 6–9% higher than Lanners, (iii) the minimum rate of vertical sink is 10–12% higher for Peregrines than for Lanners, (iv) Peregrines require thermals 20–26% wider than Lanners in order to soar and (v) when flying cross-country, gliding at optimum speed between thermals rising at a standard 5 m s^{-1}, Peregrines fly 1–3% faster than Lanners.

Overall, optimum flight speeds for Peregrines are higher but fuel consumption for powered flight is greater and gliding performance is inferior in terms of its sustainability in calm conditions. The Peregrine's capacity to fly cross-country is impaired by its dependence on larger thermals. In strong winds Peregrines should be able to maintain sufficiently high

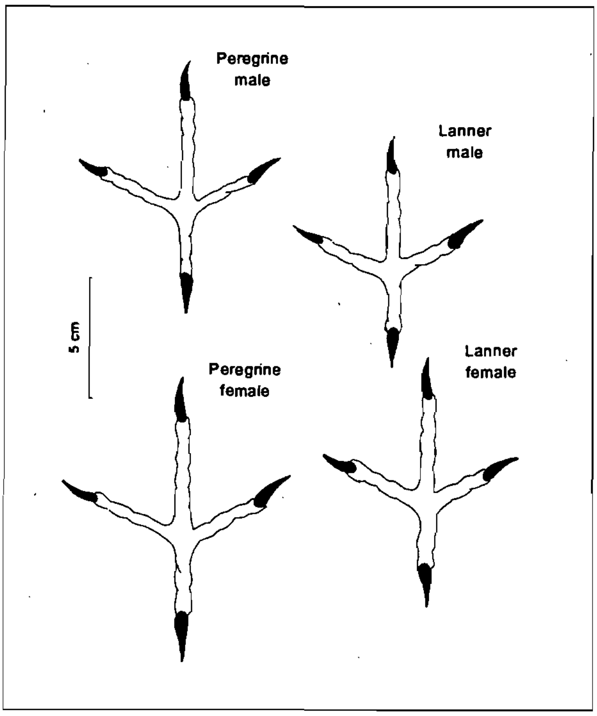

Figure 3.2 Relative foot size and proportions of southern African Peregrines and Lanners, based on the data in Appendix 5.

Table 3.3 Activity budget data for Peregrines and Lanners at the AFNP, from observations of two pairs of each species. Data for each sex were pooled within species. Peregrines n = *17 observation periods, Lanners* n = *11 observation periods. (n.s. = not significant,* *P<*0.05,* **P<*0.01,* ***P<*0.001)*

	Peregrines	Lanners	*U* value
flying[a]	4 (range 1–9)	21 (range 7–62)	182***
gliding[b]	55 (range 29–87)	53 (range 43–73)	98 n.s.
flapping[b]	40 (range 13–71)	14 (range 5–29)	172***
thermaling[b]	5 (range 0–31)	33 (range 4–48)	177***

[a]average % of time observed
[b]average % of time observed flying

air speeds and glide relatively more efficiently (Tucker & Parrot 1970). Although differences were not significant, immatures tended to have slower optimum flight speeds, higher lift:drag ratios and glide ratios, slower stall speeds and narrower circling radii than adults, and flight tended to be less energetically expensive.

Observed flight performance

Peregrines remained almost exclusively within the confines of the gorge, and were in sight for 78.5% of the total observation time, whereas Lanners frequently flew out of sight over the country adjacent to the gorge, and were in sight for only 50.5% of the observation time. Including time when two birds were under observation at once, and excluding time when no birds were in sight, 119.8 h of activity budget data were collected at Peregrine sites (males 58.9 h, females 60.9 h), and 68.0 h at Lanner sites (males 34.8 h, females 33.2 h). Because observation samples were small for the sexes within each species, data were pooled and activity budgets were compared between species only. Observation periods where birds were in sight for less than 60 min ($n = 1$ at Peregrine sites, $n = 2$ at Lanner sites) were excluded from the analysis. Of the total samples, Peregrines flew for 4.7 h (3.9%) and Lanners for 11.4 h (16.8%). Seventy-three flights and 25 strikes were measured at Peregrine sites, covering 94.2 km. Eighty-five flights and 41 strikes were measured at Lanner sites, totalling 123.4 km of flying. Mean maximum temperatures for Peregrine (26.5 ± 6°C, $n = 17$) and Lanner (25.5 ± 3°C, $n = 11$) observation periods used in the activity budget analyses were not significantly different ($t_{26} = 0.77$, $P > 0.2$), and the modal wind speed ranks were the same (mode = 1: light wind).

Peregrines flew significantly less than Lanners (Table 3.3), and when flying, flapped significantly more and soared in thermals significantly less. Temperature did not obviously influence the flight behaviour of either species. On average, Peregrines flew faster and for shorter periods than Lanners (Table 3.4). Peregrines (especially males) made strikes over longer distances and at greater speeds than Lanners, and had higher wingbeat frequencies. Peregrines flew significantly more, and while flying flapped significantly less, in windy conditions than in calm conditions (Table 3.5). Wind speed did not significantly influence Lanner activity budgets. Mean Peregrine flight distance indices were significantly greater in windy conditions than in calm conditions (calm = 790 m, windy = 1743 m, $t_{53} = 3.63$, $P < 0.001$) and their flights were longer in duration (calm = 64 s, windy = 141 s, $t_{41} = 2.54$, $P < 0.02$). Lanner flight distances were not significantly greater in windy conditions, but flight durations were longer (calm = 64 s, windy = 141 s, $t_{39} = 2.54$, $P < 0.02$). Observed home ranges of the two Peregrine pairs (0.85 km^2 and 0.81 km^2) were smaller than those of the two Lanner pairs (1.29 km^2 and 1.13 km^2).

Peregrines hunted almost exclusively in the gorge. On two occasions they were seen slope soaring along the edge of the gorge in the late evening, making numerous, fast flights at and through loose aggregations of insectivorous bats. Five bats were caught in this way and eaten on the wing before hunting was resumed. Otherwise, of 45 discrete hunts observed at Peregrine sites, 11 (24.4%) were successful, 44 (97.8%) were perch hunts and only one (2.2%) was initiated from the air. Lanners may have hunted away from the gorge

***Table 3.4** Flight times, distances and speeds and wing beat frequency indices of male and female Peregrines and Lanners at the AFNP, from observations of two pairs of each species. Data for each sex were pooled within species. Data given are means ± SD and ranges. (n.s. = not significant, *$P<0.05$, **$P<0.01$, ***$P<0.001$)*

	Peregrines (*n*; range)	Lanners (*n*; range)	*t* value
males			
flight distance index (m)	1297 ± 1078 (33; 200–5750)	1469 ± 1083 (43; 100–4625)	0.69 n.s.
flight time (s)	126 ± 134 (24; 16–585)	269 ± 274 (26; 11–1149)	2.39*
flight speed index ($\mathrm{m\ s^{-1}}$)	13.5 ± 6.3 (24; 3.6–32.7)	7.3 ± 5.6 (26; 2.4–25.0)	3.55***
strike distance index (m)	398 ± 268 (11; 150–1100)	179 ± 137 (18; 50–600)	2.92**
strike speed index ($\mathrm{m\ s^{-1}}$)	26.7 ± 7.9 (10; 16.7–40.3)	18.9 ± 9.4 (16; 6.7–35.0)	2.20*
wingbeat frequency index (beats $\mathrm{s^{-1}}$)	4.23 ± 0.76 (176; 1.33–7.00)	3.59 ± 0.60 (170; 1.67–5.20)	8.52***
females			
flight distance index (m)	1079 ± 827 (40; 150–3175)	1263 ± 1202 (41; 200–7650)	1.43 n.s.
flight time (s)	88 ± 68 (32; 24–334)	167 ± 114 (25; 26–390)	3.23**
flight speed index ($\mathrm{m\ s^{-1}}$)	12.1 ± 1.3 (32; 4.7–21.6)	7.0 ± 3.2 (25; 3.4–14.4)	5.20***
strike distance index (m)	279 ± 190 (14; 70–675)	234 ± 94 (22; 100–400)	1.10 n.s.
strike speed index ($\mathrm{m\ s^{-1}}$)	24.9 ± 9.1 (11; 10.0–40.0)	19.5 ± 7.8 (16; 8.6–31.8)	1.65 n.s.
wingbeat frequency index (beats $\mathrm{s^{-1}}$)	3.94 ± 0.56 (182; 2.13–5.33)	3.17 ± 0.64 (127; 1.60–4.75)	11.29***

during the periods that they were out of sight. All the Lanner hunting attempts observed were made in the gorge, and they were successful in 14 out of 62 (22.6%) strikes. Of these 53 (85.5%) were perch hunts and nine (14.5%) were aerial hunts. Peregrines actively flushed prey before chasing it (see Jenkins & van Zyl 1994) in 13 (28.9%) of the observed hunts, and pairs hunted together on four occasions (8.9%). Lanners only flush-hunted four times, but pairs hunted together 27 times (6.5% and 43.5% respectively of the hunts observed). Both species hunted small birds (Redeyed Bulbuls *Pycnonotus nigricans* and Redbilled Queleas *Quelea quelea*), aerial insectivores (Alpine Swifts *Apus melba* and Rock Martins *Hirundo fuligula*) and columbids (*Streptopelia* dove spp. and Rock Pigeons *Columba guinea*). Forty-three (95.5%) of the Peregrine strikes observed apparently were attempts to make clean, aerial catches, once a small bird was snatched off the rock wall of the gorge, and once a female caught a Rock pigeon while perched, as it tried to dislodge her from a ledge (Jenkins & van Zyl 1994). Lanners attempted to catch prey in the air in 56 (90.3%) of the strikes observed, and on six occasions either struck and retrieved prey, chased it out of cover on foot or caught it on the cliff face.

Table 3.5 *Activity budgets relative to wind speed for Peregrines and Lanners at the AFNP, from observations of two pairs of each species. Data for each sex were pooled within species. Peregrines* n = *10 observation periods with calm/light winds (ranks 0 and 1) and* n = *7 observation periods with moderate to strong (ranks 4 & 5), Lanners* n = *4 and* n = *7 respectively. (n.s. = not significant,* *P<*0.05,* **P<*0.01,* ***P<*0.001)*

	calm/light wind	moderate/strong wind	*U* value
Peregrines			
flying[a]	2 (range 1–5)	6 (range 2–9)	60**
gliding[b]	50 (range 29–87)	62 (range 28–79)	51 n.s.
flapping[b]	49 (range 13–71)	27 (range 13–40)	62**
Lanners			
flying[a]	28 (range 7–62)	17 (range 7–42)	15 n.s.
gliding[b]	53 (range 29–87)	54 (range 28–79)	12 n.s.
flapping[b]	16 (range 9–28)	12 (range 5–25)	16 n.s.

[a]average % of time observed
[b]average % of time observed flying

Overall, Peregrines perched more/flew less than Lanners, flew faster and tended to flap and glide whereas Lanners glided and soared in thermals. Peregrines were more aerial in windy conditions, were more exclusively perch hunters than Lanners, and hunted over longer distances at higher speeds.

Discussion

Differences between adults and immatures

Age-related differences in morphology and flight performance have been reported for falcons previously (Beebe 1960, Amadon 1980, Cade 1982). Longer flight feathers and lighter wing loadings in immature birds are thought to function in reducing the risk of injury (Amadon 1980), increasing manoeuvrability at low speeds and reducing the energetic costs of flight in inexperienced birds (Mueller *et al.* 1981). Brown (1989) has suggested that lower wing loadings may also facilitate the dispersal of independent young away from natal territories, over habitats where flying conditions are less favourable than in areas occupied by resident adults. In this study, such age related differences were evident (Table 3.1) but mostly were not statistically significant, perhaps because individual variation was considerable and sample sizes were small.

Morphometrics, catching and killing

Prey handling abilities are related to foot and bill size in falcons (Cade 1982). The larger feet of Peregrines (Table 3.2 and Fig. 3.2) indicate that they are better equipped to catch and control prey in aerial hunts. Thomson (1984) suggests that African Peregrines are more exclusively aerial in their hunting methods than sympatric Lanners. The sample of hunts observed in this study suggest that Peregrines are more likely to catch prey in open, aerial hunts than Lanners, and that Lanners are less stereotyped in their capture techniques. Peregrines tend to have larger bills (Appendix 5), and probably have more massive bill musculature (e.g. Hull 1991), suggesting that they probably are more efficient than Lanners at quickly killing prey while still in the air after a successful aerial hunt (Cade 1982).

A higher wing loading in Peregrines (Appendix 5) may mean that they encounter more difficulty when trying to take-off from the ground than Lanners, especially if carrying prey. Certainly, lifting an equivalent weight into the air with a smaller flight-surface area is more energetically demanding. This may also contribute to the Peregrine's tendency to hunt and catch prey in exclusively aerial strikes.

Predicted vs *observed flight performance*

The flight performance information generated by Pennycuick's (1989) programs (Table 3.2), which predicted subtle but significant differences between the two species based on consistent morphometric differences, was largely confirmed by field observations (Tables 3.4–3.6). In order to minimize the energy expenditure of flight, birds should use sources of atmospheric energy as much as possible to stay in the air. Lanners are able to circle in smaller thermals than Peregrines, and apparently were able to use this source of lift to a greater extent at the AFNP, and fly for longer periods, over greater distances, and to forage from the air to a greater extent (Table 3.3). Peregrines were generally restricted to gliding and flapping flight. Energetic constraints should require that birds glide where possible rather than flap. Tucker & Parrot (1970) define two goals of gliding flight: covering distance over the ground from one point to another, and to stay in the air by static or slope soaring. Under most conditions, a bird with a higher lift:drag ratio (e.g. the Lanner) will achieve these goals more easily than one with a lower lift:drag ratio (e.g. the Peregrine). In calm conditions, Peregrines therefore should be forced to cover ground by flapping flight more often than Lanners. This apparently was the case at the AFNP (Table 3.3). In terms of fuel consumption per unit distance and per unit time flown, flapping flight is more energetically expensive for Peregrines than for Lanners. Hence Peregrines should be far less aerial than Lanners, which was the case at the AFNP. Also, theory predicts that a bird with relatively high optimum glide speeds and a relatively high sinking speed (e.g. the Peregrine) glides over distance relatively efficiently into a strong head wind (Tucker & Parrot 1970). Peregrines at the AFNP were more aerial in windy conditions (Table 3.5). Both species probably were more sedentary in the river gorge situation at the AFNP than they might be in other conditions, perhaps where prey are less spatially concentrated. For example, Peregrines on the Cape Peninsula were absent from the immediate vicinity of their home cliffs for 40–60% of the time observed (but were perched for about 90% of the time they were in sight (Jenkins 1987, Chapter 4).

Calculated optimum flight speeds are faster for Peregrines than for Lanners, and observed flight speed indices, for both flights and strikes, were also higher for Peregrines (Table 3.4). Speed indices of Peregrines were similar to absolute values measured for level flying and stooping Peregrines in other studies (about 15 m s^{-1} and 40 m s^{-1} respectively – Cochran & Applegate 1986, Alerstam 1987, White & Nelson 1991), although strike speed estimates from this study did not account for vertical distance covered and were much lower than theoretical maximum speeds (Tucker 1998). Although Peregrines tended to fly faster than predicted, and Lanners slower, flight speed indices were remarkably similar to the predicted cross-country speeds (Tables 3.3 & 3.5), especially given that air density at the AFNP (not measured) probably differed from the default value used to calculate the predicted performance parameters. Higher strike speeds by Peregrines than by Lanners are attributable mainly to differences in the wing loadings of the two species (Cade 1982, Norberg 1986). Lanners, with lighter wing loadings, should be more agile and capable of faster acceleration than Peregrines (Andersson & Norberg 1981, Norberg 1986). Observations suggest that this is not the case. In most of the hunts I recorded at the AFNP, Peregrines appeared to be more agile and quicker to respond to the evasive tactics of prey, and usually hunted singly. Lanners hunted in pairs relatively frequently, and this may have enabled them to catch birds which were generally too agile for individuals to catch easily on their own (e.g. Alpine Swifts). The higher wingbeat frequencies of Peregrines (Table 3.4), presumably attainable through a combination of smaller wings and more massive pectoral musculature than Lanners, probably account for their visibly superior aerial dexterity (Andersson & Norberg 1981, Cade 1982).

Wingbeat frequency indices were about 25% lower than values calculated using Pennycuick's (1990) equation (Peregrine males 5.33 beats s^{-1}, Peregrine females 5.15 beats s^{-1}, Lanner males 4.56 beats s^{-1} and Lanner females 4.34 beats s^{-1}), and probably even lower than actual frequencies (see Pennycuick *et al.* 1994).

Flight performance, foraging mode and habitat selection

Jaksić & Carothers (1985) found that higher wing loadings in raptors predicted a *sit-and-wait* rather than *active search* hunting mode. This suggests that Peregrines should be more sedentary hunters than Lanners, preferring to hunt from a perch rather than search for prey from the air. This was confirmed by the small sample of hunts observed in this study, and by the significant difference in the time the two species spent flying. Given the relatively high cost:benefit ratio of foraging for bird-eating raptors (Temeles 1985), additional energetic constraints on flying for Peregrines are likely to restrict foraging mode to the optimum, and increase habitat selectivity. Hence, Peregrines should be more restricted than Lanners to areas where suitably high vantage points for perch-hunting are available (e.g. mountainous areas where high cliffs are frequent). This is the case in South Africa, where Peregrine distribution follows the distribution of cliff availability more closely than sympatric Lanners, and Peregrine habitat selectivity indices are higher (Chapter 1).

Differences in the primary foraging modes of Peregrines and Lanners should result in corresponding differences in their feeding rates and diets (Huey & Pianka 1981). Also, as suggested by Norberg (1977), as sit-and-wait predators Peregrines should be more habitat selective and more sedentary in their hunting methods as food availability decreases.

The difference in the two species' abilities to utilize thermals has further implications for their respective habitat preferences and dispersal potential. Since Lanners are relatively efficient users of thermals, they may be resident in low relief areas where thermals are the primary source of lift for active search hunting and cross-country flying. In contrast, Peregrines are relatively poor users of thermals and may prefer areas of higher relief because of the slope soaring opportunities they provide (see also Pennycuick & Scholey 1984). Barnard (1986) found that a montane raptor with a higher wing loading was significantly more dependent on slope lift generated by wind for prolonged, energetically efficient foraging than a sympatric raptor with a lower wing loading. Active search hunting in Peregrines probably is similarly constrained.

There is evidence for local migratory movements of southern African Lanners (Steyn 1982, van Zyl *et al.* 1994), but none has been reported for Peregrines. This may be because African Peregrines are less efficient flyers over low relief areas, and these may act as barriers to their dispersal. Northern races of the Peregrine are known to migrate over long distances, and to live and breed in areas of relatively low relief. However, aspect ratios in these birds may be higher, and wing loadings lighter in relation to their size, making cross-country flying relatively less energetic. Estimates of the minimum aerobic scope required for flapping flight presented by Pennycuick *et al.* (1994) for a male and a female Peregrine, presumably of North American origin, were 12.5 and 16.8 respectively for an air density of 1 kg m^{-3}. Equivalent values for average southern African Peregrines are 17.0 and 19.3 suggesting that in relative terms, powered flight is about 20% more strenuous.

Differences in the morphology and flight performance of southern African Peregrine and Lanner Falcons correspond to differences in their feeding ecologies, distribution and abundance. The greater degree of morphological specialization in Peregrines means that, although they are better adapted to the high speed, open aerial pursuit of birds than Lanners, they are less efficient in other hunting and flying modes and less able to exploit other food sources. Thus, in poor food areas Peregrines may either be absent or restricted to habitats which particularly favour their specialized hunting techniques. Lanners are less likely to be restricted in this way.

In a morphometric study of the genus *Falco*, Kemp & Crowe (1991) found that smaller, tropical races of Peregrines (e.g. *F. p. minor* and *F. p. peregrinator*) are relatively stocky, short tailed, short winged and large footed, and group with the morphologically extreme Orangebreasted *F. deiroleucus* and Taita Falcons *F. fasciinucha*, whereas larger, northern races (e.g. *F. p. pealei*) have relatively longer wings and tails, and are more closely allied to the desert or hierofalcons (Cade 1982) (e.g. *F. biarmicus*). Hence, morphological differences of a similar nature to those illustrated here for southern African Peregrines and Lanners, and with similar functional, behavioural and ecological implications, may occur between different races of *F. peregrinus*, as well as between Peregrines and congeners in other parts of the world. This may partly explain broad-scale patterns of distribution and abundance of large falcons.

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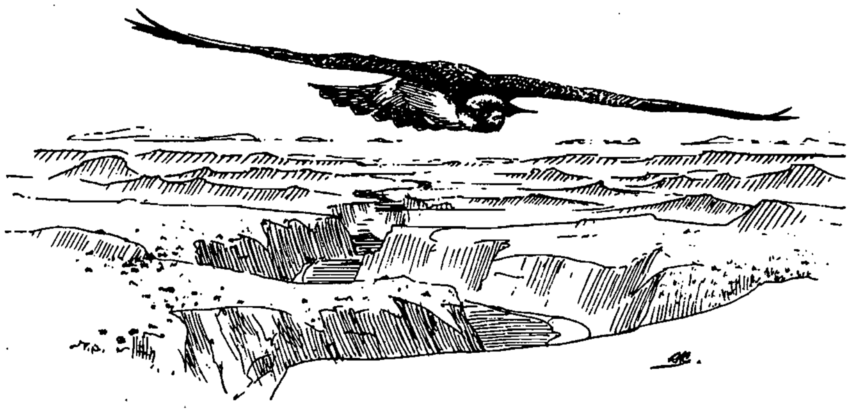


Chapter Four

Hunting mode and success of African Peregrines: does nesting habitat quality affect foraging efficiency?

"...feathers hit the ground before the weight can leave the air..." (Michael Stipe & REM, Fall on me *from* Life's rich pageant*, IRS Records 1987)*

Summary *– Peregrine hunting behaviour was studied at nest sites in three areas of South Africa over eight years. In Africa, resident Peregrines are mostly restricted to high cliffs, possibly because these structures provide optimal conditions for hunting. This hypothesis is examined in terms of the influence of nest site quality, particularly cliff height, on foraging efficiency. Over 2300 bird-hours of observation were accumulated and over 1300 hunts were detailed. Foraging mode and the design of hunts varied considerably between sites. Males foraged more actively than females, otherwise there was little variation in hunting behaviour between sexes, seasons or study areas. Individually, Peregrines spent 30–50% of the day in the vicinity of the nest cliff, and ranged more widely in warm or windy conditions when flight was less energetically costly. On average, about 0.5 hunts were recorded per hour of observation. Foraging mode was not correlated with cliff height or elevation, but Peregrine pairs occupying higher cliffs achieved higher hunting success rates. Most hunts were initiated from elevated perches on the nest cliff, and perch hunts were more successful than strikes made from the air. Success was highest in strikes at doves and small passerines, and over habitats with moderate cover. The height difference between Peregrine and prey at the start of a hunt significantly affected hunting success. Overall, Peregrines were relatively sedentary and made extensive use of the nesting habitat as a foraging area. High nest cliffs contributed to foraging success by providing perch-hunting falcons with an effective height advantage over their prey.*

Introduction

The Peregrine is a morphologically and behaviourally specialized predator of birds (Cade 1982, del Hoyo *et al.* 1994, Chapter 3). Peregrines hunt from elevated perches or high soaring positions, and use their relatively heavy bodies and streamlined shape to descend in rapid dives and strike or catch flying prey in mid-air (Cade 1982, Ratcliffe 1993). Breeding pairs are usually found in areas where cliffs or similar structures are available as nesting sites and vantage points for hunting (Cade 1982, Ratcliffe 1993).

This chapter describes the foraging behaviour of Peregrines in South Africa. African Peregrines are non-migratory (Mendelsohn 1988, Chapter 1), and the activities of territorial pairs are centred on the nest cliff throughout the year (Chapter 1). In many areas resident pairs are restricted to particularly high cliffs (e.g. Tarboton & Allan 1984, Chapter 2) which are rare in

Table 4.1 Variables used to describe Peregrine hunting attempts

1. Number and sex of the falcon/s involved: single male, single female or pair together.
2. Falcon's point of origin: perched or flying.
3. Prey's point of origin: perched and flushed by falcon, or flying.
4. Perch or flying height: vertical height above the surrounding terrain (for aerial hunts, estimated at the perceived starting point of the strike) (m).
5. Relative height: for perch hunts only – perch height as a proportion of the highest locally available perch (in most cases the top of the nest cliff) (%).
6. Distance to prey: horizontal distance from falcon's perch or position in the air at the start of the hunt, to prey (m).
7. Prey height: prey's vertical height above the ground at the point of interception (m).
8. Height difference: vertical distance between the falcon's perch or position in the air at the start of the hunt, and the point of interception (m).
9. Identity of prey: species, type or general description, including information on relative size – small (sparrow size or smaller), small-medium (starling size), medium (small dove size), medium-large (large dove size) or large (pigeon size or larger).
10. Flock size: estimate of the number of birds in the hunted flock at the start of the hunt.
11. Number of passes: how many attempts did the falcon make to catch the prey during the hunt, including the initial strike?.
12. Intensity of the hunt: subjective assessment according to the character of the approach, the strike and the falcon's subsequent behaviour (high, medium/indistinguishable, or low).
13. Success: was prey secured? Yes or no.
14. Habitat: subjective assessment of the availability of refuge for prey in the habitat over which the hunt took place – sparse cover (open sea, desert, sandy shore), moderate cover (open woodland, suburban), dense cover (forest, closed woodland, urban).
15. Reason for failure: if prey was not caught, how did it escape? (e.g. prey was caught but then dropped by the falcon, prey outflew the falcon, prey dived into cover before the falcon could could close with it).

the environment. It has been suggested that high cliffs present optimal hunting conditions for Peregrines (Beebe 1974, Tarboton 1984, Jenkins 1988, Mearns & Newton 1988), and that such foraging advantages may be prerequisite for successful breeding in African conditions (Tarboton 1984, Jenkins 1991). Two predictions of this hypothesis are examined here, namely (1) that Peregrines frequently hunt in the vicinity of the nest cliff and (2) that the physical structure of the nesting habitat affects hunting success.

Methods

Peregrine foraging behaviour was observed from 1989–1996 at eight sites on the Cape Peninsula, four sites along the lower Orange River and four sites in the Soutpansberg. Three of the Cape Peninsula sites were on low to moderate cliffs with steep scree slopes, overlooking a mosaic of urban, forest and heathland habitats, four were on moderate to high cliffs overlooking the sea and one was on a tall building in the industrial suburbs of Cape Town. Two sites on the Orange River were in a deep, rocky gorge and two sites were on high cliffs overlooking the river. Peregrines in the Soutpansberg used moderate to high cliffs with steep, wooded scree slopes overlooking a flat savanna plain.

Observations and sampling effort

Observations of Peregrine behaviour were made using 10x40 binoculars or a 20–60x spotting scope, from points 200–400 m from the nest cliff. All activities were recorded and timed to the nearest minute. The birds were observable within about a 2 km radius of the nest cliff, depending on the topography of the site. No attempt was made to follow foraging birds when they flew out of sight. While newly fledged Peregrines frequently were observed at their natal cliffs late in the breeding season, only observations of territorial adults are included in this study.

A total of 1761 observation periods were completed, ranging in duration from 5 min to 15 h (average 1.6 h) and comprising 2728.9 h of sampling effort. Observation periods were classed according to season (non-breeding or breeding) and time of day (early morning, mid-morning, midday, early afternoon or evening, full morning or afternoon, or full day). At active nest sites the stage in the breeding cycle during which each observation period took place was also recorded (incubation, nestling or fledgling stage). Prevailing weather conditions during each visit were assessed in terms of cloud cover (0/8–8/8 cloud), temperature (cool, mild or warm-hot) and wind strength (calm-light, light-moderate, moderate, moderate-strong or strong) and direction (compass octants). The earliest

Table 4.2 The accumulated time for which Peregrines were observed at nest sites in the three study areas, with details of the number of hunts observed at each site

site	time observed males (h)	time observed females (h)	hunts by males	hunts by females	hunts by pairs
Cape Peninsula					
PA1	264.6	371.3	130	574	52
PA2	258.5	421.4	114	121	32
PA3	55.9	62.3	20	13	17
PA4	3.8	14.0	0	3	0
PA6	11.5	21.4	1	3	0
PA7	23.1	36.5	2	3	0
PA8	84.5	101.4	9	21	4
PA13	18.3	26.3	4	6	2
subtotal	720.1	1054.5	280	744	107
Orange River					
PB1	9.8	21.4	0	7	1
PB2	18.7	34.3	3	6	0
PB3	101.2	119.5	75	36	12
PB4	36.0	43.5	10	13	5
subtotal	165.7	218.6	88	62	18
Soutpansberg					
PC2	18.5	30.3	3	2	0
PC3	10.6	28.5	1	2	0
PC4	11.6	32.2	0	1	0
PC5	14.9	45.2	0	10	0
subtotal	55.6	136.2	4	15	0

visits commenced before first light and the latest finished just after dark. Observations were spread fairly evenly through the day in the Soutpansberg and on the Orange River, but were biased towards the early morning or late evening on the Cape Peninsula, where midday watches comprised only 9% of the total observation time. Visits to Soutpansberg and Orange River sites were confined to seasonal field trips to these areas, usually to monitor breeding success, and only 8% of the Soutpansberg observations were made during the non-breeding season. Considerably more observation time was accumulated at Cape Peninsula sites which were more conveniently situated and visited regularly throughout the year.

On every visit, the accumulated time for which each bird of the resident pair was in sight, and the time for which at least one bird of the pair was in sight, was expressed as a percentage of the total observation period. The frequency with which hunts were made in the vicinity of the nest cliff was calculated for each individual, and for the pair combined, as the number of hunts seen per hour of observation at each site. These measures of cliff attendance and hunting rate were assumed to reflect the extent to which the nest cliff was used as a foraging site by the male and female independently, and by the pair together.

Hunting data

Only clearly observed attempts by Peregrines to flush (Hustler 1983, Jenkins & van Zyl 1994) or strike prey were considered as hunts. Depending on how completely the build-up to a strike was seen, each hunting attempt was summarized by a maximum of 15 variables (Table 4.1). These identified the participants, described their position relative to one another at the start of the hunt, and detailed the hunting strategy of the Peregrine and the evasive tactics of its intended prey. Not all Peregrine strikes appear to be genuine attempts to catch prey (Cade 1982, Ratcliffe 1993). Some may constitute play behaviour (Czechura 1984) or hunting practice (Dekker 1980, Treleaven 1980), or may be intended to test the reaction and capabilities of potential prey before a more determined attack is made (Roalkvam 1985). In order to account for varying levels of motivation in estimates of hunting success, hunts were classed according to a subjective assessment of 'intensity' (see Treleaven 1980). 'High intensity' hunts were typically preceded by periods of alert scanning or

Table 4.3 *Average cliff attendance (time in sight as a percentage of observation time) and hunting rate (number of hunts seen per hour of observation) figures comparing males and females of pairs, breeding and non-breeding seasons for birds of each sex and the three study areas for birds of each sex (n.s. = not significantly different,* $^{*}P<0.05$, $^{***}P<0.001$*)*

	males	females		Wilcoxon Z
pairs ($n = 16$)				
% attendance	26.6	39.7		3.54***
hunts per hour	0.08	0.14		2.18*
	breeding	non-breeding		Wilcoxon Z
males ($n = 5$)				
% attendance	38.7	36.5		0.54 n.s.
hunts per hour	0.25	0.12		2.16*
females ($n = 5$)				
% attendance	49.1	48.3		0.54 n.s.
hunts per hour	0.30	0.29		0.27 n.s.
	Cape Peninsula	Orange River	Soutpansberg	Kruskal-Wallis H
males	($n = 8$)	($n = 4$)	($n = 4$)	
% attendance	25.7	30.8	24.2	0.42 n.s.
hunts per hour	0.08	0.14	0.02	2.57 n.s.
females	($n = 8$)	($n = 4$)	($n = 4$)	
% attendance	36.1	44.0	42.7	1.61 n.s.
hunts per hour	0.18	0.14	0.06	4.20 n.s.

patrolling, followed by rapid, direct, aggressive strikes at prey, with multiple passes if required. 'Low intensity' hunts were less purposeful and more opportunistic, often involved falcons which had recently fed (with visibly full crops), and usually comprised relatively slow strikes at prey, with few, if any, repeat passes. After unsuccessful high intensity hunts, Peregrines usually resumed hunting. Unsuccessful low intensity hunts were often followed by bouts of unassociated behaviour. Bird heights and strike distances were estimated in relation to the height of the nest cliff and a working knowledge of the spatial geography of each site based on 1:5000 aerial photos or 1:50 000 topographic maps.

Although Peregrines hunted aerial prey in conspicuous situations, the speed with which strikes were made and the distances over which they took place often compromised detailed observation, reducing the sample sizes obtained for many variables. Hunts were easier to see at some sites than at others, and numerous possible hunts which were completed out of view were not included in the analysis. In this way, observability affected estimates of hunting rate, and probably biased the sample of recorded hunts in favour of shorter strikes at high-flying prey (e.g. pigeons), and at the expense of longer strikes at typically low-flying prey (especially doves). This problem was particularly prevalent in the Soutpansberg where tall vegetation often hampered visibility.

Table 4.4 Estimates of the height and elevation of nest cliffs where foraging behaviour was observed, and average cliff attendance, hunting frequency and hunting success data for Peregrine pairs at each site

site	cliff height/elevation (m)	% attendance	hunts per hour	% success
Cape Peninsula				
PA1	100/100	69.3	1.06	7.5
PA2	100/200	68.7	0.35	13.9
PA3	200/400	35.6	0.22	16.0
PA4	100/200	17.3	0.02	0.0
PA6	70/500	41.8	0.06	0.0
PA7	40/310	45.0	0.05	0.0
PA8	70/270	58.0	0.14	8.8
PA13	60/290	37.7	0.14	8.3
Orange River				
PB1	110/250	37.0	0.19	50.0
PB2	140/140	44.2	0.04	22.2
PB3	90/90	76.3	0.60	19.5
PB4	120/120	51.7	0.30	46.4
Soutpansberg				
PC2	180/580	55.1	0.18	20.0
PC3	100/350	31.9	0.05	0.0
PC4	120/320	52.0	0.01	0.0
PC5	80/230	58.6	0.15	0.0

Statistical analyses

The data generally were not normally distributed, so non-parametric statistical tests were used throughout. Cliff attendance and hunting rate data were pooled for each individual. Differences in these parameters between males and females of pairs, and seasonal differences within individuals of each sex (only for sites with at least 50 h of observation time per season), were examined using Wilcoxon paired-sample tests (Zar 1984). Kruskal-Wallis one-way analysis of variance (ANOVA) was used to examine within-sex differences between the three study areas, and within-area variation in cliff attendance and hunting rate data for each pair combined. Thereafter, data for all observation periods were pooled.

Data describing hunts were pooled for each individual or pair hunting together for which samples of 10 or more hunts were obtained. Paired-sample tests were used to investigate differences between males and females of pairs, and between single-bird hunts (with data for males and females pooled) and tandem hunts at each site. Averages were calculated for each site at which 20 or more strikes were observed. These data were combined for each area, and differences between areas were examined using ANOVA, after which data for all hunts were pooled.

Results

Overall, 2350.6 bird-hours of observation were accumulated (Table 4.2), 941.4 h for males and 1409.3 h for females. A total of 1318 hunting attempts were observed, 372 by males alone, 821 by females and 125 were by both members of the pair (Table 4.2).

Variation between sexes, sites and study areas

Females were present at the nest cliff for a greater proportion of each observation period than males, and more hunts by females were seen per hour of observation than by their mates (Table 4.3). Males showed no seasonal variation in cliff attendance, but hunted in the vicinity of the nest cliff more frequently in the breeding season (Table 4.3). Cliff attendance and hunting frequency were not seasonally variable for females, and did not vary significantly between the three study areas for birds of the same sex (Table 4.3). There was significant variation in cliff attendance and hunting rates between sites in each study area (Table 4.4). This was most marked on the Cape Peninsula (cliff attendance: Kruskal-Wallis H = 192.59, $P<0.001$; hunting rate: H = 185.45, $P<0.001$, n = 8), less so on the Orange River (cliff attendance: H = 19.93, $P<0.001$; hunting rate: H = 27.33, $P<0.001$, n = 4) and marginal in the Soutpansberg (cliff attendance: H = 8.18, P =

0.04; hunting rate: $H = 3.09$, $P = 0.38$, $n = 4$).

Males hunted smaller birds in larger flocks than females, and pairs hunted smaller birds in larger flocks than Peregrines hunting alone (Tables 4.5 & 4.6). Also, pairs made high intensity strikes relatively more frequently than individuals (Table 4.6). Otherwise, hunts by males *vs* females of pairs, and by individuals within pairs *vs* pairs hunting together, were not significantly different for most variables (Tables 4.5 & 4.6). Overall, males and females achieved equal success in strikes at small birds (males 51.7% of 58 hunts *vs* females 46.4% of 28 hunts, χ^2_1 with Yates' correction = 0.05, $P = 0.82$); but females hunted large prey more successfully than males (males 1.2% of 172 hunts *vs* 8.7% of 602 hunts by females, $\chi^2_1 = 10.39$, $P = 0.001$). No significant differences were found in the design and success of hunts between the three study areas, although the number of sites compared was small and variation between sites in each area was considerable (e.g. Table 4.4).

Foraging mode

Cliff attendance and hunting rates of Peregrine pairs were not significantly correlated with cliff height (cliff attendance: Spearman's rank correlation coefficient $r_s = -0.15$, $n = 16$ sites, $P = 0.57$; hunting rate: $r_s = 0.13$, $n = 16$, $P = 0.62$) or elevation (cliff attendance: $r_s = -0.44$, $n = 16$, $P = 0.09$; hunting rate: $r_s = -0.36$, $n = 16$, $P = 0.16$, data from Table 4.4).

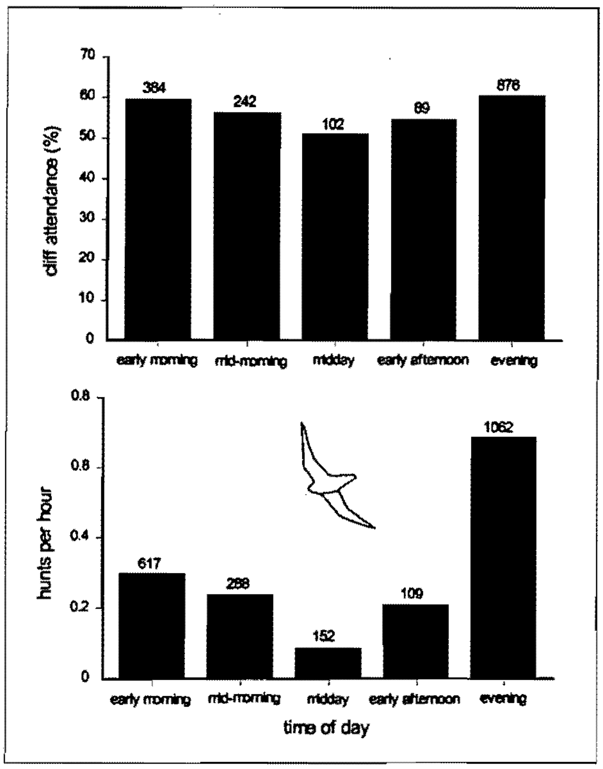


Figure 4.1 Peregrine cliff attendance and hunting rates in relation to time of day. The number of observation periods completed (upper graph) and the number of hours of observation accumulated (lower graph) for each time period in the day are indicated at the top of each bar.

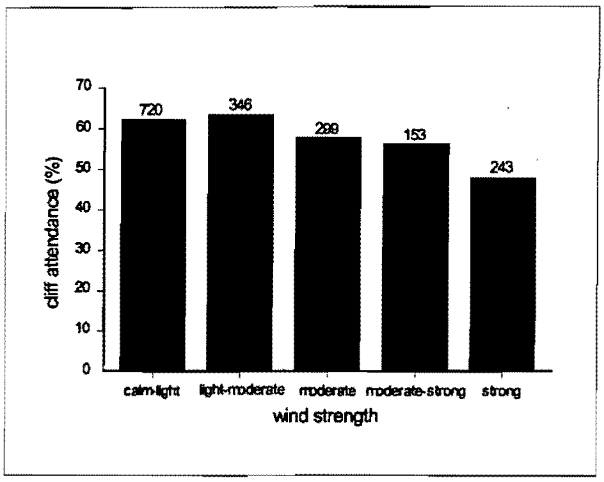


Figure 4.2 Peregrine cliff attendance and hunting rates in relation to estimated wind strength. The number of observation periods completed for each wind strength category are indicated at the top of each bar.

With the data for all observations pooled, males and females spent, on average, 33.3% and 48.2% of the day respectively in the vicinity of the nest cliff. At least one bird of a pair was in attendance at the cliff for 59.3% of each observation period, and an average of 0.47 strikes were recorded per hour of observation. Cliff attendance and hunting frequency were highest in the early morning and evening and lowest over midday (Fig. 4.1). At active nest sites hunting frequency increased from 0.22 hunts per hour of observation during incubation ($n = 202.9$ h), to 0.32 hunts per hour during the nestling stage of the cycle ($n = 352.1$ h), and peaked at 0.55 hunts per hour when pairs were supporting large or fledged young ($n = 233.0$ h). About 70% of the hunts observed were initiated from a perch.

There were no significant correlations between foraging mode and prevailing weather conditions (cf. Chapter 3), although cliff attendance tended to decrease with increasing wind strength (Fig. 4.2; $r_s = -0.90$, $n = 5$ wind categories, 1761 observation periods, $P = 0.07$), suggesting that Peregrines extended their foraging ranges on windy days.

The design of hunts

Most hunts began with shallow to steep dives punctuated by short bursts of rapid flapping flight with half-flexed wings. Once sufficient speed was attained the falcon flattened out its approach and closed in directly behind and slightly below the flight path of its prospective prey. Very few long, vertical dives at prey were seen, and the majority of successful hunts involved clean catches rather than glancing blows followed by attempts to retrieve dead or injured prey. Peregines hunted from vantage points 25–600 m above the surrounding terrain, and over horizontal distances of 20–2000 m. Prey were attacked at altitudes of 1–500 m above the ground, and strikes were initiated at birds flying from 400 m above the hunting falcon to 500 m below it. Flocks of 1–200

Table 4.5 *Average data (with ranges in parentheses) comparing hunts by males and females of Peregrine pairs (n = 5 pairs, n.s. = not significantly different,* *$P<0.05$*)

variable[a]	males	females	Wilcoxon Z
% hunts from a perch	66.8 (50.0–78.2)	65.2 (58.3–72.5)	0.27 n.s.
% hunts at flying birds	78.3 (61.1–91.1)	64.8 (33.3–89.2)	1.62 n.s.
perch/flying height (m)	150 (78–284)	155 (73–332)	0.27 n.s.
distance to prey (m)	355 (265–535)	369 (247–456)	0.54 n.s.
prey height ground (m)	70 (49–134)	74 (40–139)	0.54 n.s.
relative height (%)	80.4 (65.0–88.8)	82.8 (80.0–85.9)	0.27 n.s.
height difference (m)	85 (33–142)	88 (32–203)	0.27 n.s.
% hunts 'high intensity'	33.5 (20.2–70.0)	24.2 (15.4–30.8)	0.81 n.s.
% hunts at large birds	46.8 (25.6–80.6)	69.1 (37.5–90.0)	2.01*
% hunts at small birds	50.0 (15.3–68.9)	26.2 (0.0–62.5)	2.01*
flock size	16.6 (1.4–36.1)	1.6 (1.0–2.4)	1.89 n.s.
% success	21.2 (0.0–70.0)	15.5 (7.7–23.1)	0.81 n.s.

[a] see Table 4.2 for full definition of each variable

birds were targeted, and from 1–30 passes were made per hunting attempt. With the data for all hunts pooled, over 80% of the total sample were strikes made at flying birds, the remainder being attempts to flush stationary prey.

Hunting success

Average hunting success correlated significantly with nest cliff height ($r_s = 0.53$, $n = 16$ sites, $P = 0.04$) but not with total elevation ($r_s = -0.30$, $n = 16$, $P = 0.24$, data from Table 4.4). Aerial hunts were less successful than perch hunts (7.9% of 330 hunts *vs* 16.1% of 741 hunts, $\chi^2_1 = 13.04$, $P<0.001$), flush hunts were less successful than direct strikes at flying prey (3.8% of 210 hunts *vs* 15.0% of 874 hunts, $\chi^2_1 = 17.38$, $P<0.001$) and low intensity hunts were less successful than high intensity hunts (1.8% of 218 hunts *vs* 41.1% of 353 hunts, $\chi^2_1 = 100.53$, $P<0.001$). There was no difference in success between single and multiple pass hunts (11.8% of 1050 hunts *vs* 12.6% of 198 hunts, $\chi^2_1 = 0.04$,

Table 4.6 *Average data (with ranges in parentheses) comparing hunts by individual Peregrines and hunts by pairs (n = 4 sites, n.s. = not significantly different,* *$P<0.05$*)

variable[a]	individuals	pairs	Wilcoxon Z
% hunts from a perch	64.5 (56.0–72.6)	73.5 (66.0–83.3)	1.28 n.s.
% hunts at flying birds	72.0 (55.5–89.50)	94.2 (88.2–100)	1.64 n.s.
perch/flying height (m)	173 (91–310)	182 (82–346)	0.36 n.s.
distance to prey (m)	372 (250–489)	416 (271–588)	0.91 n.s.
prey height (m)	89 (60–137)	103 (28–218)	0.80 n.s.
relative height (%)	81.8 (74.1–86.4)	83.9 (79.4–89.2)	1.28 n.s.
height difference (m)	116 (32–179)	97 (34–154)	0.27 n.s.
% hunts 'high intensity'	24.2 (22.9–26.1)	46.9 (31.3–82.4)	2.01 *
% hunts at large birds	61.2 (40.5–86.9)	28.1 (0.0–81.3)	2.01 *
% hunts at small birds	33.7 (9.3–50.9)	61.6 (16.7–83.3)	2.01 *
flock size	9.1 (2.0–23.2)	27.1 (3.0–57.6)	2.01 *
% success	11.2 (3.0–18.9)	18.6 (1.9–41.2)	0.73 n.s.

[a] see Table 4.2 for full definition of each variable

Table 4.7 The number of Peregrine hunts observed at different avian prey types, with the average flock size, the average number of passes made, the relative incidence of low intensity strikes and hunting success at each type

prey group	number of hunts seen	flock size	number of passes	% low intensity	% success
doves[a]	20	1.4	1.4	5.0	50.0
small birds[b]	82	7.1	1.5	0.0	42.7
small-medium birds[c]	90	8.7	1.8	12.2	17.8
aerial insectivores[d]	84	40.1	4.8	20.2	16.7
pigeons[e]	810	1.5	1.3	20.0	7.0
medium to large birds[e]	47	2.1	1.6	29.8	0.0

[a]small columbids, low-flying, mostly *Streptopelia* sp.; [b]mostly sparrows and queleas; [c]mostly starlings and weavers; [d]swifts, swallows and martins; [e]large columbids, high-flying, *Columba* sp.; [f]mostly ducks, small raptors and waders

$P = 0.84$). Success was highest over midday (24.1% of 54 hunts) and lowest in the evening (7.9% of 768 hunts).

Capture rates in the breeding and non-breeding seasons did not differ significantly (9.9% of 593 hunts *vs* 12.6% of 725 hunts, $\chi^2_1 = 1.94$, $P = 0.16$). However, at active nest sites, hunting success rose from 4.4% during incubation (n = 45 hunts) to 10.7% during the nestling stage (n = 112 hunts) and 15.7% during the fledgling stage of the breeding cycle (n = 127 hunts).

Peregrines hunted medium-sized and small prey (especially doves and small passerines) more successfully than larger species (Table 4.7). Most exploratory, low intensity hunts were made at particularly aerial or large prey species (e.g. swifts and pigeons). Aerial insectivores, medium to large birds and pigeons stayed airborn and outflew Peregrines in 93.5% (n = 31), 71.4% (n = 21) and 44.3% (n = 183) respectively of unsuccessful hunts at these quarry. In contrast, doves, small birds and small-medium birds evaded hunting Peregrines by diving into cover in 100% (n = 3), 73.3% (n = 30) and 57.9% (n = 19) respectively of unsuccessful strikes. Attempts at isolated individuals of each of the major prey types (small birds, small-medium birds, aerial insectivores and pigeons) were more successful than hunts at flocks of two or more birds (average success rates = 33.3% and 15.3% respectively, Wilcoxon paired-sample $Z = 2.00$, $n = 4$ prey types, $P = 0.04$). Five hunts at large, flying insects were recorded, and 11 hunts at bats, all of which were successful.

Hunting success was highest over sparse and moderate cover habitats and lowest over dense cover (Table 4.8). Prey avoided capture by finding refuge in hunts over moderate cover but not over sparse and dense cover habitats, where low intensity hunts were most frequent (Table 4.8). Peregrines were seen using cover to approach and surprise prey in only 31 hunts (2.4% of the total sample).

Of the physical parameters estimated for each strike, the initial height difference between Peregrine and prey (excluding strikes made at birds flying higher than the hunting falcon) contributed significantly to hunting success, both in terms of hunts made from perches on the nest cliff only (Fig. 4.3; $r_s = 1.00$, $n = 5$ height

Table 4.8 Details of Peregrine hunts observed over different habitats, including the proportion of strikes where prey found refuge, the relative incidence of low intensity strikes and hunting success

habitat[a]	number of hunts seen	% refuge found	% low intensity	% success
sparse cover	77	3.7	16.9	26.0
moderate cover	51	70.6	0.0	29.4
dense cover	757	4.5	18.0	8.1

[a]see Table 4.2 for full definition of each habitat category

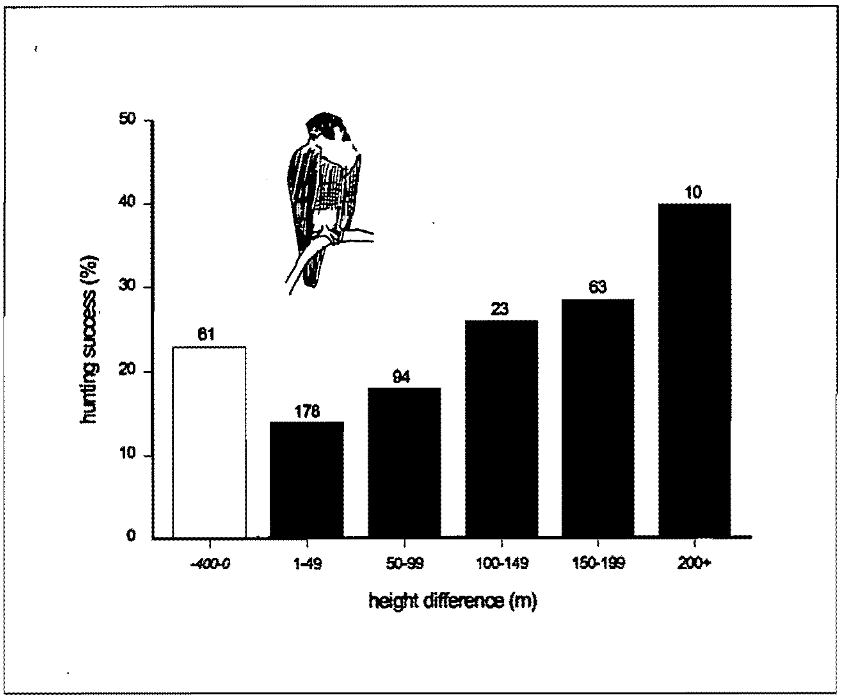


Figure 4.3 Peregrine hunting success in perch hunts in relation to the vertical height difference between falcon and prey at the start of the hunt. Sample sizes (number of hunts seen) for each height difference category appear at the top of each bar.

difference categories, 368 strikes, $P<0.001$) and perch and aerial hunts combined ($r_s = 1.00$, $n = 5$ height difference categories, 405 strikes, $P<0.001$). Attempts at high-flying prey were infrequent and usually involved rapid, climbing flights culminating in long, downward strikes. These energetic hunts were probably only made at particularly vulnerable prey, hence Peregrines were relatively successful in these situations (Fig. 4.3) without the benefit of an initial height advantage. Height difference was the only variable which was significantly different between successful and unsuccessful, directly downward strikes (successful $n = 78$, average height difference = 98 m, unsuccessful $n = 327$, average height difference = 74 m, Mann-Whitney $Z = 2.79$, $P = 0.005$). Falcon perch height at the onset of each strike ($r_s = 0.90$, $n = 5$ perch or flying height categories, 854 strikes, $P = 0.07$) and prey height at the point of interception ($r_s = -0.90$, $n = 5$ prey height categories, 533 strikes, $P = 0.07$) may have affected hunting success, and the horizontal distance over which strikes were made tended to increase with perch or flying height ($r_s = 0.90$, $n = 5$ perch or flying height categories, 687 strikes, $P<0.07$). However, these relationships were not statistically significant.

Discussion

The nesting habitat as a foraging area

Average cliff attendance and strike rate figures recorded during this study (Tables 4.3 & 4.4) confirm that South African Peregrines are relatively sedentary (also see Chapter 3) and make extensive use of the nesting habitat as a foraging area. At some sites in particular, individuals were present on or near the nest cliff for over 75% of the day and made more than one strike per hour at birds in the immediate vicinity. Significantly, Peregrines hunted more frequently close to the nest cliff, with greater success, during the critical stages of the breeding cycle when energy demands on provisioning males were greatest.

If high nest cliffs provide Peregrines with superior foraging options, the relative importance of the nesting habitat in the hunting schedule of resident pairs might be expected to vary in relation to cliff height. However, this study revealed no significant correlations between hunting mode and cliff height or elevation, probably because only a small number of nest sites were considered and foraging conditions were different at each. In particular, prey abundance was likely to vary between sites, affecting the incidence of hunting opportunities and strikes. Hence, pairs occupying low sites (e.g. PA1, PB3 and PC5 – Table 4.4) were relatively sedentary and made frequent strikes in the vicinity of the nest site, presumably in response to high local prey abundance, while pairs on high sites in less food-rich areas (e.g. PA3, PB1 & PC2) foraged more actively and made fewer strikes close to the nest cliff.

The proportion of observed hunts which were initiated from perches on the nest cliff is typical of breeding pairs throughout the species' range (Table 4.9). In contrast, Peregrines dispersed away from breeding areas may hunt mostly from the air in order to exploit prey aggregations in habitats where opportunities for perch hunting are limited (e.g. Dekker 1980, Cresswell 1996, Table 4.9). Although much of the time between hunts by Peregrines in these situations may be spent perched, the overriding trend is towards a more active foraging mode (cf. Cresswell 1996) than that employed by resident pairs (e.g. Treleaven 1980, Sherrod & Cade in Cade 1982, Bird & Aubry 1982, Chapter 3, this Chapter). While wintering Peregrines may hunt more energetically, and their success rate is lower than that of breeding pairs (Table 4.9), they often hunt larger prey

Table 4.9 *Hunting success and foraging mode of resident and migrant Peregrines in different parts of the world (also see Roalkvam 1979, Cade 1982, Temeles 1985)*

location	number of hunts seen	% success	% perch hunts	main prey
Breeding pairs at the nest site				
France[a]	400	9.3	75	various
South Africa[b]	251	12.7	63	various, pigeons
Wales[c]	113	15.9	-	pigeons
Australia[d]	32	31.0	-	various, grebes
Tunisia[e]	237	32.5	58	swallows, small birds
Canada[f]	218	33.5	75	various, jays
England[g]	55	61.8	60	pigeons
North America[h]	183	84.1	-	jays
Adult pairs at the nest site – non-breeding season				
South Africa[b]	690	12.2	74	various, pigeons
Individuals or pairs away from the nest site – non-breeding season				
Sweden[i]	252	7.5	-	various migrants
Canada[j]	674	7.7	1	waterfowl, shorebirds
Fiji[k]	74	9.7	-	pigeons
Scotland[l]	254	9.8	17	shorebirds, larks
Central African Republic[m]	87	63.2	-	queleas, small birds

References: [a]Monneret 1973 – >1 pair, [b]this study – five pairs, [c]Parker 1979 – one pair, [d]Sherrod in Cade 1982 – one female, [e]Thiollay 1988 – five pairs, [f]Bird & Aubry 1982 – one pair, [g]Treleaven 1980 – >1 pair, [h]Cade & Sherrod in Cade 1982 – one male, [i]Rudebeck 1951 – >1 individual, [j]Dekker 1980 – >1 individual, [k]Clunie 1976 – one adult female, [l]Cresswell 1996 – 8 individuals, [m]Ruggiero 1991 – one adult pair

with much higher energy returns (e.g. Dekker 1980, 1995). Breeding pairs which regularly hunt from the nest cliff generally exploit aerial or 'commuter' prey species (e.g. columbids, migrants, aerial insectivores – see Chapter 5). This complies with optimal foraging theory, which suggests that sit-and-wait predators should favour active, widely foraging prey (Huey & Pianka 1981).

Evidence for energetic constraints

Peregrines were often absent from the vicinity of the nest site, presumably on foraging flights, between about 11h00 and 14h00 (Fig. 4.1). The timing of these flights could be in response to improved thermaling opportunities during the hottest part of the day. Indications that wind strength affected the incidence of foraging flights away from the nest cliff (Fig. 4.2) support the contention that windy conditions facilitate aerial foraging, which is otherwise energetically constrained by the Peregrine's specialized morphology (Chapter 3). Alternatively, strong winds may somehow inhibit prey availability, forcing the falcons to search for prey more actively. Lower cliff attendance and hunting rate figures for males than females throughout the year (e.g. Fig. 4.2) suggest that males fly more and forage further from the nest cliff. Telemetry data from the Cape Peninsula confirm this (Jenkins & Benn 1998). Males have higher aspect ratios and lower wing loadings than females (Chapter 3), and can probably fly longer distances while sustaining lower energy costs.

Targets and tactics

The tendency for males to hunt smaller birds than females (Table 4.6) was in keeping with theories on the selective advantage of reversed sexual dimorphism (Andersson & Norberg 1981, Temeles 1985). Male African Peregrines are considerably smaller and over 30% lighter than females (Chapter 3) and struggle to carry large prey. On two occasions during this study males were observed catching pigeons which they subsequently dropped, apparently because they were too heavy to carry to a safe perch. Presumably because of their greater aerial manoeuvrability (Andersson & Norberg 1981), males were more likely than females to make solo hunts at small, agile prey such as swifts. Previous studies have reported a similar tendency for male Peregrines to target smaller prey than females (e.g. Parker 1979, Thiollay 1988).

While Peregrines hunted in pairs on a number of occasions, there was little evidence to suggest active cooperation between males and females in terms of accepted criteria, e.g. division of labour, communication to coordinate movements, sharing of prey (Hector 1986). Tandem hunts were particularly effective when directed at agile prey, and pairs achieved a higher success rate than individuals in strikes at swifts (23.8% *vs* 3.8%). This was apparently because two birds attacking together effectively doubled the number and frequency of passes made, and prey rapidly became tired, disorientated and, ultimately, easier to catch.

Hunting success rates at different prey groups by Peregrines in this study (Table 4.7) are comparable to those recorded for breeding pairs of *F. p. brookei* hunting migrants on the coast of Tunisia (Thiollay 1988), and reveal a similar capacity to catch particular types of birds. These Mediterranean Peregrines were most successful in strikes at small passerines (46%) and doves (41%), and least successful in hunts at aerial insectivores (16%).

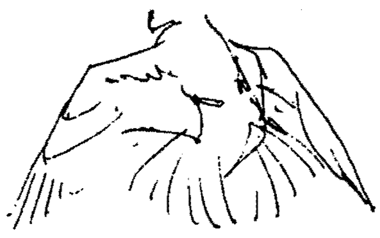
The nesting habitat and foraging efficiency

Although the Soutpansberg, the Orange River and the Cape Peninsula present markedly different environments, the foraging behaviour of Peregrines in these areas was essentially the same. The physical structure of the nesting habitat used by each pair profoundly influenced the way in which they hunted (also see Monneret 1973), and varied from site to site but not consistently between study areas.

While Peregrines were rarely seen using cover to surprise prey (cf. Dekker 1980, Cresswell 1996), low-level attacks in which cover may have been effective were difficult to observe and many were not seen to completion. Hunting success was highest in moderately vegetated habitats (Table 4.8) where prey regularly used *protective* cover to evade attacks, perhaps because Peregrines were able to use the same vegetation as *obstructive* cover (Lazarus & Symonds 1992) to mask their approach and take prey by surprise. Descriptions of strikes made by Peregrines hunting over woodland suggest that this might be the case (e.g. Hustler 1983, Czechura 1984, Ruggiero 1991), which could account for the Peregrine's documented preference for wooded habitats in many parts of the Afrotropics (Tarboton & Allan 1984, Mendelsohn 1988, Chapters 1 & 2).

A positive relationship between nest cliff height and hunting success largely confirms the influence of nesting habitat structure on Peregrine foraging efficiency. However, interpretation of this result is confounded by the lack of correlation between strike success and the total elevation of each site. This discrepancy may best be explained in terms of the falcons' access to the prey base. The elevation of each site was often a function of the height (and length) of the scree slope underlying the nest cliff (e.g. sites in Table 4.3 where cliff height is less than 50% of elevation). Particularly long scree slopes provided elevation but did not provide vertical airspace proximal to the cliff which hunting falcons could exploit.

Perhaps the most significant result of this study is the demonstration of a positive relationship between the vertical height advantage of a perch-hunting Peregrine over its prospective prey, and the probability of a successful hunt (Fig. 4.3). Falcons hunting from high cliffs enjoy a more extensive outlook than those using lower sites, and presumably have a better appreciation of targets to select and tactics to employ (Tarboton 1984, Mendelsohn 1988, Mearns & Newton 1988). Most importantly, however, they have a height advantage (maintained at no energetic cost) which enables them to achieve extreme velocities in downward strikes (Tucker 1998) to overhaul and surprise prey more effectively. For example, in some of the higher, longer strikes observed during this study, Peregrines conceivably reached theoretical maximum speeds in excess of 100 m s^{-1} (Tucker 1998). Thus, the height of the nest cliff directly affects hunting success and, all other contributing factors being equal, Peregrine pairs occupying high cliffs are likely to forage more efficiently (and breed more successfully – e.g. Mearns & Newton 1988, Chapter 7) than pairs on low cliffs.



Chapter Five

The diet of breeding Peregrines and Lanners in South Africa

"... "That's cool," said Zaphod, "we'll meet the meat." " (Douglas Adams, The restaurant at the end of the universe, *Pan Books 1980)*

***Summary** – The diet of breeding Peregrines and Lanners in South Africa was determined from analyses of prey remains collected at nest sites. Direct observations suggested that remains under-sampled small prey by about 10% and over-sampled large prey by about 8%. Peregrines and Lanners preyed predominantly on birds. Pigeons and* Streptopelia *doves comprised the bulk (38–66% by frequency; 68–85% by mass) of Peregrine prey in each of three study areas. Columbids were supplemented by starlings on the Cape Peninsula, sandgrouse and swifts on the Orange River, and mousebirds in the Soutpansberg. Cape Peninsula Peregrines had the least diverse diet, the narrowest feeding niche, and took the largest proportion of juvenile birds. Peregrines on the Orange River had the broadest feeding niche, and preyed mainly on 'commuter' species rather than sedentary residents. Lanners in the Soutpansberg took mainly terrestrial or cursorial species, particularly young Domestic Chickens* Gallus gallus *(40%; 37%) and charadriids, but columbids were also important. The diet of sympatric Peregrines and Lanners overlapped by about 35%. Peregrines concentrated on woodland and cliff-dwelling prey, while Lanners took mainly open-country species. Close neighbouring pairs of congeners did not obviously affect the food-niche parameters of Peregrine or Lanner pairs, suggesting that the two species were not actively competing for food.*

Introduction

Raptor populations are at least partly limited by the availability of food (Newton 1979). Information on the diet of birds of prey is therefore essential to an understanding of their basal resource requirements. This chapter describes the diet of breeding Peregrines and Lanners in South Africa, and examines the type and diversity of prey taken by Peregrines in different environments. The food habits of the Peregrine have been well researched in Arctic (e.g. Hunter *et al.* 1988, Rosenfield *et al.* 1995) and north temperate regions (e.g. Mearns 1983, Ratcliffe 1993) and in southwestern Australia (e.g. Pruett-Jones *et al.* 1981, Marchant & Higgins 1993). However, Peregrine diets in the tropics are poorly known, and data for African Peregrines are limited (Mendelsohn 1988). The only significant studies of Lanner diet are from the northern periphery of the species' range, in southern Europe (Massa *et al.* 1991), the eastern Sahara (Goodman & Haynes 1992) and Israel (Yosef 1991). Although the Peregrine shares many parts of its extensive distribution with other large falcon species which have similar resource needs (Cade 1982), few studies have compared Peregrine diets with those of sympatric congeners (e.g.

***Table 5.1** Samples of prey remains collected each year at falcon nest sites in three areas of South Africa. The MNI totals are the sum of prey individuals identified from skeletal remains, pluckings and macro-remains identified* in situ *and discarded. Remains collected from consecutive years were pooled where sample sizes were small*

year	number of collections	number of sites	NISP	MNI			
				skeletal	pluckings	discarded	total
Cape Peninsula Peregrines							
1989	8	1	318	37	3	22	62
1990	11	4	608	83	6	8	97
1991	7	2	187	33	8	0	41
1992	11	5	412	65	6	1	72
1993	10	5	546	63	10	1	74
1994	22	7	417	88	30	0	118
1995	7	4	161	44	4	1	49
Overall	76	10	2649	413	67	33	513
Orange River Peregrines							
1989–90	7	5	680	102	10	0	112
1991–92	4	4	410	72	8	1	81
1993–95	4	2	333	48	7	0	55
Overall	15	7	1423	222	25	1	248
Soutpansberg Peregrines							
1988–90	5	4	245	36	6	4	46
1991	13	6	719	113	8	0	121
1992	13	5	378	89	5	0	94
1993	14	4	585	93	10	0	103
1994–95	4	3	225	41	2	0	43
Overall	49	7	2152	372	31	4	407
Soutpansberg Lanners							
1991	14	9	178	65	5	0	70
1992	15	7	302	62	3	0	65
1993	10	7	188	38	0	1	39
Overall	39	9	668	165	8	1	174

Cade 1960, Porter & White 1973). This paper defines the feeding niches of Peregrines and Lanners in an area of sympatry and measures the extent to which their diet overlaps.

Methods

Prey remains were collected, and the food habits of breeding falcons were observed, at Peregrine sites on the Cape Peninsula and on the lower Orange River from 1989–95, and in the Soutpansberg from 1988–95. Comparative data on the diet of sympatric Peregrines and Lanners in the Soutpansberg was collected from 1991–93.

Prey remains

Prey remains were collected from falcon nest ledges and from below roost sites and feeding perches. Uneaten macro-remains, regurgitated pellets and plucked feathers were used in combination to minimize bias in estimates of falcon diet (e.g. Simmons *et al.* 1991, Oro & Tella 1995). Collections were made from just after egg-laying to soon after fledging. The frequency of collections varied between sites, between years and between areas (Table 5.1). Care was taken to remove all material at each collection to prevent duplication in subsequent samples. Pellets were broken up mechanically with tweezers and individual bone remnants were separated from the feather matrix. The sorted material is retained in the comparative prey sample collection at the South African Museum, Cape Town.

The condition of the skeletal remains varied. Older bones were a feature of first collections and were bleached and weathered after prolonged exposure to the elements. However, most of the material was fresh and well preserved, often with several bones still articulated. Breakage and other damage varied widely according to the size of prey species, the degree to which bones had been torn apart during feeding and whether they had been ingested or not. Ingested bones regurgitated in pellets were almost invariably damaged by exposure to gastric acid. Often, however, the feather matrix of pellets buffered bones against acid erosion sufficiently to allow at least gross-level identification. Incompletely ossified bones (considered to be those of juveniles), or bones of small species, were those most severely damaged and eroded.

All avian osteological material was identified with the aid of comparative skeletons in the South African Museum and additional material loaned from the Transvaal Museum, Pretoria and the National Museum, Bloemfontein. Individual body parts were separated according to taxon and recorded as the Number of Identified Specimens (NISP). The Minimum Number of Individuals (MNI) was calculated from the most common body part among the NISP identified for each species, after accounting for paired elements, using the methods outlined in Klein & Cruz-Uribe (1984). This technique of quantification, using cranial and post-cranial elements, is routinely used by many zooarchaeologists and was used in the analysis of recent avian prey remains by, for example, Avery *et al.* (1985) and Boshoff *et al.* (1994). Mammal remains were identified on cranio-dental characteristics by D.M. Avery of the South African Museum.

Bird and mammal remains were identified to the lowest possible taxonomic level. All prey individuals were assigned to a size class, based on bone size in the case of unidentified prey, and on body mass data from the literature (Brown *et al.* 1982, Maclean 1993, Smithers 1983) where individuals were identified at least to family. Size classes were: small (up to sparrow size, average about 20 g), small–medium (starling size, average about 60 g), medium (dove size, average about 130 g), medium–large (large dove size, average about 220 g), large (pigeon size and larger, average about 350 g) and very large (francolin size and larger, average about 600 g). In biomass calculations, unidentified prey were given these average mass values. Mean body mass values from the literature were used for prey identified to species. Prey identified only to higher taxonomic levels were assigned mass estimates based on published weights of similar or related forms.

Arthropod, amphibian and reptile remains were few and were identified at a gross level only. Arthropods were recorded as fragments of exoskeleton recovered from pellets. A small number of mostly non-avian remains were considered as unlikely prey of falcons, particularly Peregrines, on the basis of size or habit. These are included on lists of collected remains (Appendix 6) but were excluded from the NISP and MNI figures and from subsequent diet analyses. Some relatively complete, easily identifiable prey remains were identified in the field and discarded. These are not reflected in the NISP data and, to avoid duplication, only contribute to the total number of identified prey where fewer individuals of the relevant taxon were subsequently identified from other remains in the corresponding collection.

Pluckings were identified using the bird study-skins collection in the South African Museum. No attempt was made to determine the number of individuals represented by the sum of pluckings of a particular species collected in each sample. To prevent duplication in the samples, species identified from feather remains contributed one individual to the total for a collection, but only when the relevant taxon was not recorded in the skeletal remains. Juveniles were identified from plumage characteristics where these differed from adult birds, and from the predominance of sheathed or incompletely grown tail or flight feathers which indicated that nestling or recently fledged individuals had been taken.

Observations

Limited data on falcon diet observed in the field are used here primarily to detect bias in the analyses of prey remains (e.g. Collopy 1983, Rosenberg & Cooper 1990). Nearly 1000 h of breeding season observations were completed at Peregrine nest sites on the Cape Peninsula, and over 200 h each at Peregrine sites on the Orange River and in the Soutpansberg and at Lanner sites in the Soutpansberg. Observations were made using 10x40 binoculars or a 20–60x spotting scope from distances of 200–400 m. Whenever a falcon was seen with food, an effort was made to identify or at least estimate the size of its prey. Size classes used were the same as those applied to prey remains. Only largely intact prey could be identified or size-classified.

Diet breadth and overlap

Indices of diet breadth and overlap were calculated in terms of the relative frequency of taxa identified in prey remains. This was done at the species level wherever possible to refine the quality of these food-niche parameters (Greene & Jaksić 1983, Sherry 1990). Diet breadth (B_A) was calculated using Levins' (1968) standardized formula:

$$B_A = B - 1/\mathrm{n} - 1, \text{ where } B = 1/\sum p_i^2$$

where p_i is the proportion of the diet contributed by the *i*th taxon. Values of B_A range from 0 to 1, with larger values indicating a broader diet. Also, the 'number of frequently used taxa' (those comprising 3% or more of the total number of identified prey – Krebs 1989) was tallied for each falcon population as an additional estimate of diet breadth. Diet overlap was measured using Morisita's (1959) index of similarity:

$$C = 2\sum p_{ij}p_{ik} / \sum p_{ij}[(n_{ij}-1)/(N_j-1)] + \sum p_{ik}[(n_{ik}-1)/(N_k-1)]$$

where p_{ij} and p_{ik} are the proportions taxon i makes up of the diets of species j and k respectively, n_{ij} and n_{ik} are the number of individuals of taxon i in the diets of species j and k respectively and N_j and N_k are the total number of individuals in the diets of species *j* and *k* respectively. Values of *C* range from 0 to 1, with larger values indicating a greater dietary overlap. This index is considered the least prone to biases associated with sample size and the number of resources used (Smith & Zaret 1982). Multivariate cluster analyses were conducted to examine qualitative differences in the diet of sympatric Peregrines and Lanners, using the PRIMER software package (Plymoth Marine Laboratory, U.K.). Diet composition data were compared using (1) the Bray-Curtis similarity coefficient (using group average linking) to generate a dendrogram of hierarchical clusters, and (2) a process of non-metric multidimensional scaling to generate an ordination plot.

To examine the possible competitive influence of nearby Lanner pairs on the diet of Soutpansberg Peregrines and *vice versa*, the food niche parameters of falcon pairs with congeners as close neighbours (Peregrines $n = 3$, average distance to nearest Lanner pair = 0.6 km, Lanners $n = 4$, average distance to nearest Peregrine pair = 0.7 km) were compared with those of relatively isolated pairs (Peregrines $n = 4$, average distance to nearest Lanner pair = 6.5 km, Lanners $n = 5$, average distance to nearest Peregrine pair = 4.7 km).

Prey availability

Two sampling techniques were used to estimate the abundance and distribution of potential avian prey in the vicinity of falcon nest sites, with a view to making qualitative assessments of prey selection and habitat use. A rough estimate of local prey availability was made at falcon nest cliffs by counting the number of potential prey per hour which flew across a sampling area prescribed by a 1 m^2 frame. This frame was positioned at the top of the cliff, looking out and down, or on the scree slope below the face looking up at the crest. An observer sat 2 m behind the frame, looking through it, to make the count. Prey passage rate counts were made at different times of the day at a cross-section of the falcon sites on the Cape Peninsula and in the Soutpansberg only, mostly from 1991–93.

Line-transect counts were walked in the

***Table 5.2** The three species most frequently recorded in prey remains collected at Peregrine and Lanner nest sites in each year of the study, and the combined percentage of the diet which they comprised. Only species which were recorded from two sites or more in each year or combination of years were considered. Where two species were taken with equal frequency the largest was ranked first*

year	most frequent prey species in order of importance	% of diet
Cape Peninsula Peregrines		
1989	Redeyed Dove, Cape Turtle Dove, Laughing Dove	67.8
1990	Cape Turtle Dove, Laughing Dove, Redeyed Dove	50.5
1991	Laughing Dove, European Starling, Feral Pigeon	48.7
1992	Laughing Dove, European Starling, Cape Turtle Dove	68.1
1993	Laughing Dove, European Starling, Rock Pigeon	58.2
1994	Laughing Dove, European Starling, Feral Pigeon	58.5
1995	Laughing Dove, European Starling, Rock Pigeon	75.4
Orange River Peregrines		
1989–90	Rock Pigeon, Bradfield's Swift, Namaqua Sandgrouse	34.8
1991–92	Redeyed Dove, Namaqua Sandgrouse, Laughing Dove	21.4
1993–95	Rock Pigeon, Namaqua Sandgrouse, Feral Pigeon	47.3
Soutpansberg Peregrines		
1988–90	Rock Pigeon, Cape Turtle Dove, Feral Pigeon	32.6
1991	Laughing Dove, Speckled Mousebird, Redeyed Dove	36.4
1992	Laughing Dove, Redfaced Mousebird, Redeyed Dove	50.0
1993	Laughing Dove, Redfaced Mousebird, Rock Pigeon	37.9
1994–95	Laughing Dove, Redfaced Mousebird, Redeyed Dove	58.1
Soutpansberg Lanners		
1991	Domestic Chicken, Laughing Dove, Crowned Plover	59.9
1992	Domestic Chicken, Crowned Plover, Redeyed Dove	61.6
1993	Domestic Chicken, Laughing Dove, Crowned Plover	56.5

Soutpansberg to estimate bird densities in seven habitats, identified in terms of a broad-scale classification of the character and structure of vegetation present (cf. Edwards 1983, also see Introduction). The plains to the south of the mountain range comprise either short, semi-open *savanna woodland* or short, sparse *denuded woodland*, often found adjacent to rural settlements and heavily impacted by clearing and cultivation. *Forest & plantation* includes tall, closed stands of both indigenous evergreen and exotic eucalypt or pine forest. Areas of montane *grassland & scrub forest* are typical of the upper slopes of the mountains and feature low, open grassland with patches of short deciduous forest. *Deciduous woodland* comprises short, moderately closed woodland and occurs on the northern backslopes and on the middle and upper slopes at the west end of the range. The lower scree slopes of the escarpment are thickly vegetated, with low, closed woodland or *moist thornscrub* in the east and short, moderately closed woodland or *dry thornscrub* further west. One or two sites were selected as typical of each habitat type and at least three 1 km line-transects were walked at these sites each breeding season from 1991–1993. Transect sites were located between 150 m and 3 km from the main escarpment. Transects were completed at various times of day, but mostly in the morning or in the late afternoon. The transects were walked briskly, so only the birds which were conspicuously active in the area, and hence most likely to provide falcons with hunting opportunities, were recorded. High, overflying birds and species considered too large for falcons to catch and subdue under normal circumstances (>800 g in weight) were not counted. The species, number of individuals and approximate perpendicular distance from the transect line (e.g. Bibby *et al.* 1992) were recorded for each sighting.

Results

A minimum of 1168 individuals of at least 82 species from 34 families were identified as prey from the

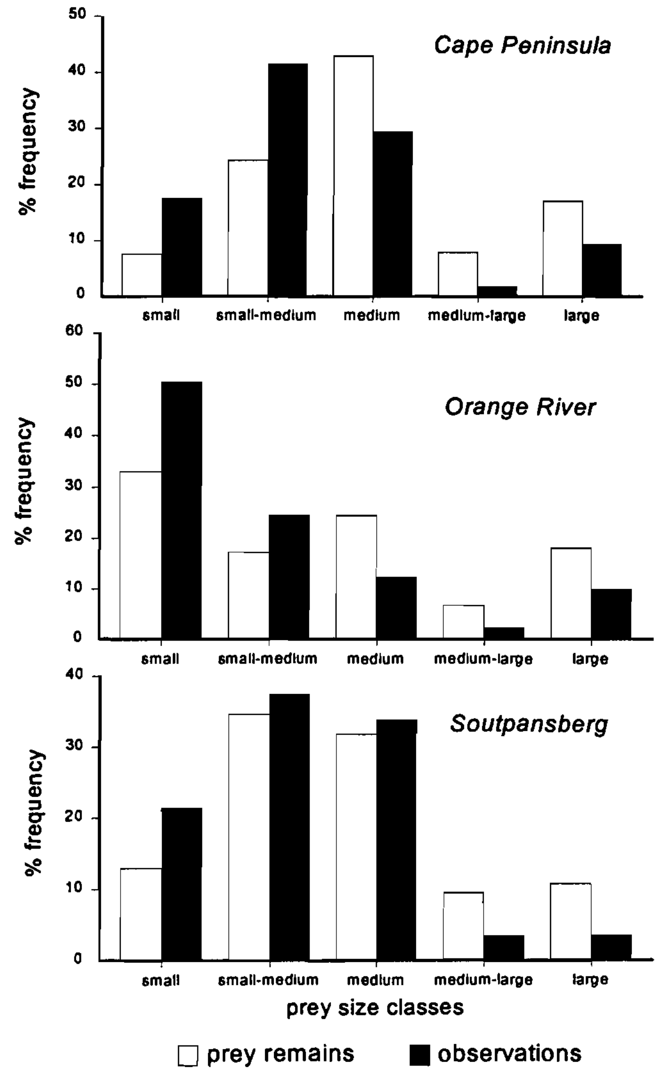


Figure 5.1 The relative frequency of prey of different size classes in the diet of Peregrines in three areas of South Africa, determined from the analysis of prey remains and direct observations. Prey remains differed significantly from observations on the Cape Peninsula (remains n = *513, observations* n = *159,* χ^2_4 = *42.0,* P<*0.001) and on the Orange River (remains* n = *248, observations* n = *81,* χ^2_4 = *14.0,* P = *0.007) but not in the Soutpansberg (remains* n = *407, observations* n = *56,* χ^2_4 = *7.3,* P = *0.12).*

remains collected at Peregrine nest sites (Table 5.1, Appendix 6), and a minimum of 174 individuals of at least 24 species from 15 families were identified from Lanner prey remains (Table 5.1, Appendix 6). Samples of remains collected at Peregrine sites in the Soutpansberg from 1991–93 were more substantial than those from sympatric Lanner sites, yielding more specimens per collection (Peregrines average = 45.6, range 2 – 211, n = 47 collections, Lanners average = 18.6, range 1 – 60, n = 36 collections, Mann-Whitney Z = 3.01, P = 0.003) and more identified individuals per collection (Peregrines average = 8.0, range 1 – 31, n = 49 collections, Lanners average = 4.5, range 1 – 10, n = 39 collections, Z = 2.77, P = 0.006).

Peregrines were observed catching or feeding on 296 prey individuals (Appendix 7), about half of which could be identified at least to family. Fifteen species from eight families were recognized. Only 36 prey individuals were identified during observations at Lanner sites in the Soutpansberg. These comprised one locust, one 1–3 day old Domestic Chicken (the scientific names of all prey species mentioned in the text are provided in Appendices 6–8), one *Streptopelia* dove, one unidentified murid, seven unidentified small birds, nine small–medium birds, 12 medium birds and four medium–large birds.

Prey remains vs *observations*

Because relatively few prey items were identified in the field, and the sample of observed prey at Lanner sites was so small, the quality of the diet information provided by the analysis of prey remains could only properly be assessed in terms of the size of prey observed at Peregrine sites in each area (Appendix 7). These comparisons (Fig. 5.1) suggest that remains collected on the Cape Peninsula provided the least accurate diet estimate, while those from sites in the Soutpansberg were the most accurate. On average, prey remains under-represented smaller prey by about 10% and over-represented larger prey by about 8%. Taxonomically the samples were similar, with birds, and particularly columbids, predominating in all (Appendices 6 & 7).

Falcon diet

The relative importance of key species in falcon diets was fairly consistent between years (Table 5.2), so prey remains data for each year were pooled. There was some variation in the early years of the study at Peregrine sites on the Cape Peninsula and in the Soutpansberg. The greater durability of the remains of large columbids, and a resulting bias towards these species in the first/oldest samples collected at each nest site, may account

Table 5.3 *Summary of Peregrine diet from the analysis of prey remains collected at nest sites (see Appendix 1 for raw data). The importance of each taxon is expressed in terms of its relative frequency in the sample of individuals (%f) and in terms of its contribution to the total biomass of prey in each sample (% m). Families comprising 1% or more of the diet in each sample are listed. Cape Peninsula* n *= 513 individuals, 74107 g, Orange River* n *= 248 individuals, 31811 g, Soutpansberg* n *= 407 individuals, 50193 g*

Family	Cape Peninsula		Orange River		Soutpansberg	
	% f	% m	% f	% m	% f	% m
Phasianidae	-	-	-	-	1.5	3.6
Charadriidae	1.0	-	-	-	3.9	5.3
Glareolidae	-	-	-	-	1.0	-
Laridae	-	-	2.4	2.1	-	-
Pteroclidae	-	-	9.7	14.0	1.0	1.9
Columbidae	66.1	85.1	37.5	69.9	48.2	68.4
Psittacidae	1.0	-	-	-	-	-
Apodidae	6.2	1.9	10.1	4.1	6.1	2.9
Coliidae	1.0	-	1.2	-	13.5	6.1
Alaudidae	-	-	7.7	1.0	1.0	-
Hirundinidae	-	-	6.1	-	-	-
Sturnidae	15.0	8.2	1.6	1.4	3.2	2.3
Ploceidae	4.5	1.1	4.4	-	4.2	1.0
Estrildidae	-	-	1.2	-	-	-
Fringillidae	-	-	1.6	-	1.0	-
Molossidae	-	-	6.5	-	-	-
Pteropodidae	-	-	-	-	1.5	1.6

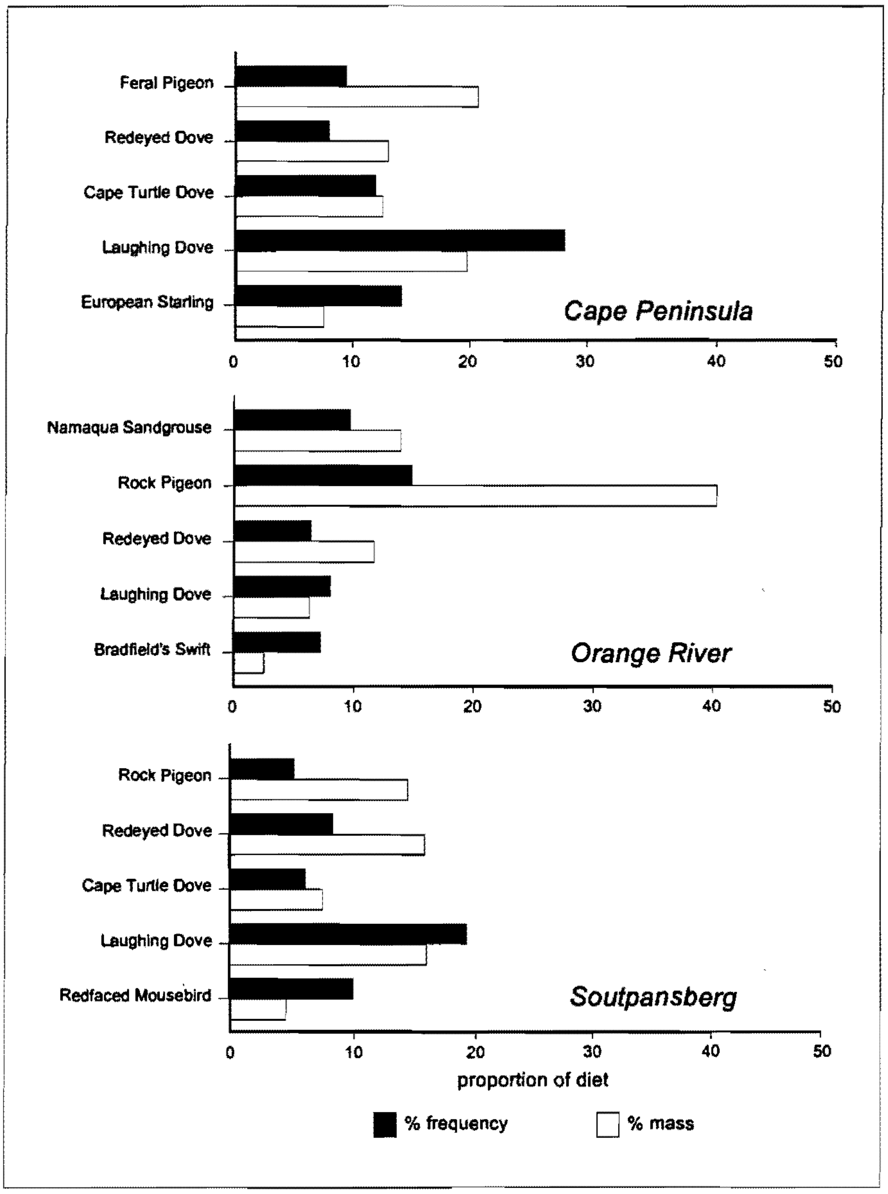


Figure 5.2 The five most important prey species in the diet of Peregrines in each study area (see Table 5.3 for sample sizes).

for this. The diet of Peregrines on the Orange River seemed to be the most variable from year to year (Table 5.2). On average, the three most frequently taken species in each year together accounted for about 40–60% of falcon diet in each area (Table 5.2).

Laughing Doves and other *Streptopelia* species featured prominently in prey remains from Peregrine sites in all three areas (Appendix 6, Fig. 5.2). Doves were supplemented variously by starlings, pigeons, mousebirds, sandgrouse or swifts. During 1991–93 Peregrines in the Soutpansberg preyed mostly on *Streptopelia* doves and mousebirds, while sympatric Lanners took Domestic Chickens, doves and Crowned Plovers (Fig. 5.3).

The relative importance of juvenile birds in the diets of Peregrines in the three study areas varied significantly ($\chi^2_2 = 19.5$, $P<0.001$). Most of the juveniles recorded were columbids (Appendix 6). Juveniles were more frequent in the diet of Peregrines on the Cape Peninsula (32/513 individuals or 6.2%) than in the Soutpansberg (3/407 or 0.7%; χ^2_1 with Yates' correction = 15.3, $P<0.001$), and comprised 3.2% of the diet of Peregrines on the Orange River. The relative frequency of juveniles in the diet of Cape Peninsula Peregrines increased through the breeding season, from 1.7% by frequency in late October to 6.2% in early November, 6.8% in late November and 8.1% in early December. A high proportion of the remains recovered from Lanner nests were young chickens. Hence, juvenile birds comprised 39.7% of identified prey from Lanner sites.

In summary, columbids made up the majority of prey taken by Peregrines in all three study areas (Tables 5.3 & 5.4). Other consistently important taxa were Apodidae, Sturnidae and Ploceidae. Soutpansberg Lanners took mainly phasianids, charadriids and columbids (Table 5.4). The average size of prey taken by Peregrines in each of the three study areas varied (Kruskal-Wallis $H = 26.8$, $P<0.001$). Cape Peninsula Peregrines took significantly larger prey (average mass = 144.5 g, range 15 – 390 g, $n = 513$ individuals) than

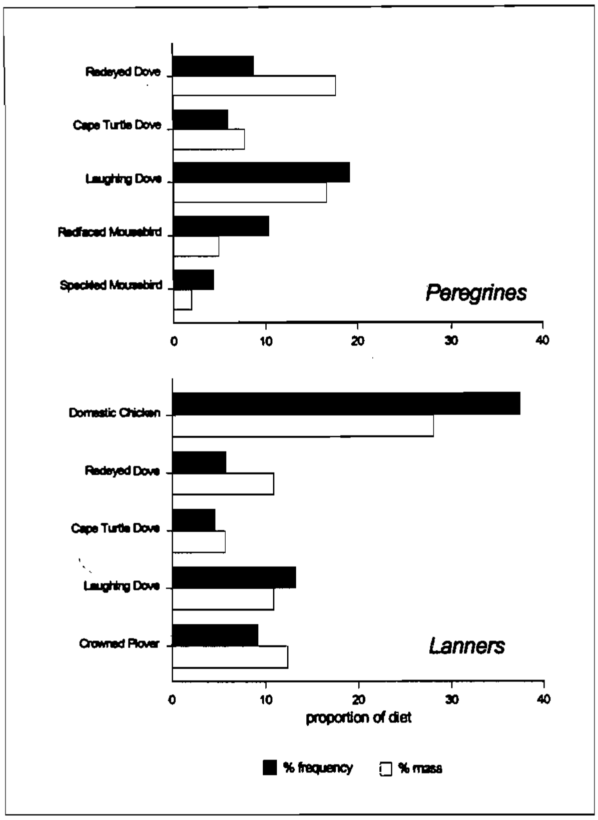


Figure 5.3 The five most important prey species in the diet of Soutpansberg Peregrines and Lanners from 1991–93 (see Table 5.4 for sample sizes).

Orange River Peregrines (average mass = 128.3 g, range 3 – 347 g, *n* = 248 individuals; Mann-Whitney $Z = 4.33$, $P<0.001$) and Peregrines in the Soutpansberg (average mass = 123.3 g, range 3 – 600 g, *n* = 407 individuals; $Z = 4.11$, $P<0.001$). On average, Soutpansberg Peregrines took significantly smaller prey than sympatric Lanners (Peregrines average mass = 116.9 g, range 3 – 600 g, *n* = 318 individuals; Lanners average mass = 123.7 g, range 3 – 500 g, *n* = 174 individuals; $Z = 2.41$, $P = 0.02$). Peregrine diet included a greater proportion of small and large prey individuals, while Lanners concentrated on medium-sized prey (Fig. 5.4).

Diet breadth and overlap

Of the three Peregrine populations studied, those on the Cape Peninsula had the least diverse diet (30 species were identified from prey remains – Appendix 6) and the narrowest diet breadth (Table 5.5). Peregrines in the Soutpansberg fed on a wide diversity of prey (at least 50 species) but concentrated on a few taxa and had a moderate diet breadth. On the Orange River only 38 species were taken but there was less emphasis on particular families so the diet was relatively broad-based (Table 5.5).

Overall, Peregrines in the Soutpansberg occupied a broader feeding niche than sympatric Lanners, and the diet of the two species overlapped by about 35% (Table 5.5). On a *per site* basis (excluding one Peregrine site and one Lanner site with insufficient samples) the difference in diet breadth was statistically significant (Peregrines average $B_A = 0.14$, range = 0.11 – 0.18, *n* =

Table 5.4 *Summary of Peregrine and Lanner diet in the Soutpansberg (1991–93) from the analysis of prey remains collected at nest sites (data were extracted from Appendix 1). The importance of each taxon is expressed in terms of its relative frequency in the sample of individuals (% f) and in terms of its contribution to the total biomass of prey in each sample (% m). Families comprising 1% or more of the diet in each area are listed. Peregrines* n *= 318 individuals, 37188 g, Lanners* n *= 174 individuals, 21532 g*

Family	Peregrines		Lanners	
	% f	% m	% f	% m
Phasianidae	1.3	3.6	40.2	37.4
Charadriidae	3.5	4.9	9.2	12.4
Recurvirostridae	-	-	1.2	1.6
Pteroclidae		1.3	-	-
Columbidae	46.5	67.2	28.2	39.1
Apodidae	5.4	2.7	1.2	-
Coliidae	14.8	7.0	-	-
Alaudidae	1.3	-	-	-
Sturnidae	3.1	2.1	-	-
Ploceidae	4.4	1.2	4.6	1.2
Fringillidae	-	-	1.2	-
Pteropodidae	1.3	1.4		
Muridae	-	-	1.2	-

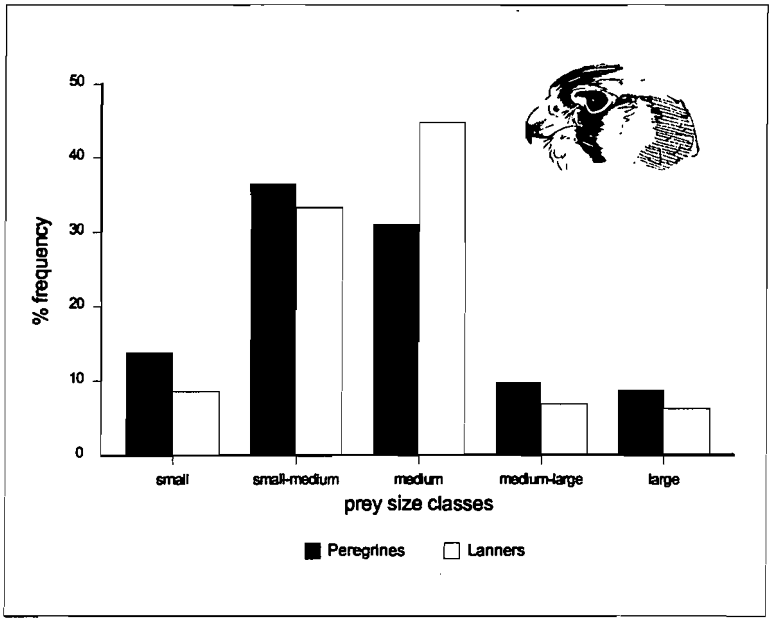


Figure 5.4 The relative proportions of prey of different size classes in the diet of Peregrines (n = 318) and Lanners (n = 174) in the Soutpansberg from 1991–93.

6; Lanners average $B_A = 0.04$, range = 0.01 – 0.14, n = 8, Mann-Whitney $Z = 2.52$, $P = 0.01$). Cluster analyses on diet composition data clearly separated Peregrine and Lanner sites (Fig. 5.5). Food-niche widths of falcon pairs with pairs of congeners as close neighbours did not differ significantly from those of more isolated pairs (Peregrines: pairs with close neighbouring Lanners average $B_A = 0.14$, $n = 3$, isolated pairs average $B_A = 0.14$, $n = 3$, Z = 1.00, P = 1.00; Lanners: pairs with close neighbouring Peregrines average $B_A = 0.08$, $n = 4$, isolated pairs average $B_A = 0.05$, $n = 4$, Z = 0.72, P = 0.47). However, collectively, interspecific diet overlap was greatest between pairs with close neighbouring congeners (close pairs $C = 0.44$, distant pairs $C = 0.26$).

Prey availability

Counts at cliffs on the Cape Peninsula and in the Soutpansberg yielded similar average prey passage rates in terms of the number of individuals counted (Cape Peninsula average = 116.3 birds per hour, range 2–542 birds per hour, n = 64 counts; Soutpansberg average = 119.0 birds per hour, range 0–929 birds per hour, n = 114 counts). A significantly greater biomass of birds per hour was recorded in counts on the Cape Peninsula (average = 8567 g per hour, range 405–33 479 g per hour, n = 64 counts) than in the Soutpansberg (average = 7104 g per hour, range 0–56 669 g per hour, n = 114 counts; Mann-Whitney $Z = 3.09$, $P = 0.002$). Mostly cliff-dwelling species were included in these counts (Table 5.6). Larger species (Rock Pigeons, Redwinged Starlings) were more common at Cape Peninsula cliffs, whereas aerial insectivores (Alpine Swifts, Rock Martins) were more abundant in the Soutpansberg (Table 5.6).

Of the habitats identified in the Soutpansberg, the woodlands on the plain below the escarpment supported

***Table 5.5** Indices of diet breadth and overlap for Peregrines and Lanners, calculated in terms of the relative frequency of taxa identified in prey remains*

study population	number of taxa used	number of taxa >3%	diet breadth (B_A)
Cape Peninsula Peregrines	39	6	0.17
Orange River Peregrines	45	10	0.34
Soutpansberg Peregrines (overall)	63	9	0.21
sympatric Peregrines and Lanners, Soutpansberg (1991–1993)			
Peregrines	67	10	0.20
Lanners	67	6	0.07
diet overlap: $C = 0.34$			

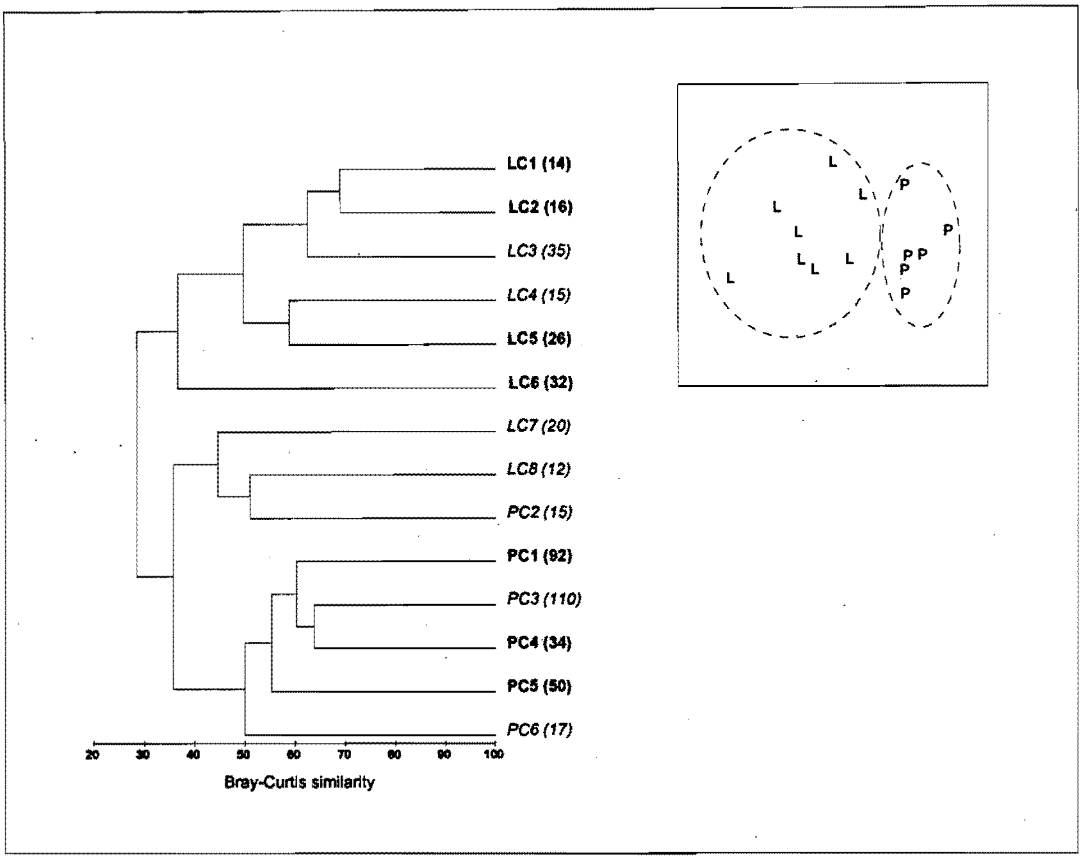


Figure 5.5 Results of cluster analyses on diet composition data for Peregrine (P) and Lanner (L) sites in the Soutpansberg. The dendrogram groups sites according to the Bray-Curtis similarity coefficient (with the number of prey individuals identified from each site in parentheses). Sites with close neighbouring pairs of congeners are italicized. The ordination plot (inset) illustrates the relatedness of each site to the others in terms of a multidimensional scaling procedure.

the highest diversity and the greatest number and biomass of birds (Table 5.7), while the dense thornscrub on the scree slopes of the mountains featured the most depauperate avifauna.

Prey and habitat selection

Some species which were recorded regularly in the diet of falcons in the Soutpansberg were not common in the environment. In particular, Redfaced Mousebirds made up about 10% of Peregrine diet by frequency (Fig. 5.2) but were not encountered on any of the transect counts (Appendix 8). Three species (Chestnutbacked Finchlark, Melba Finch and Blue Waxbill) were common on the plains at the foot of the escarpment (Appendix 8) but were infrequent or did not feature in falcon diets, perhaps because these small birds were under-represented in prey remains. Similarly, Blackeyed Bulbuls were ubiquitous in the area (Appendix 8), but were recorded as falcon prey only once (Appendix 7). There was a significant difference in the foraging habitats used by Peregrines and Lanners in the Soutpansberg, as inferred from the habitat preferences of their prey (Table 5.8). While both species favoured the wooded plains below the mountain range, Peregrines took more woodland species from relatively pristine habitats whereas Lanners took open-country species from denuded woodland and free-range chickens from around human settlements. Also, Peregrines preyed more heavily than Lanners on cliff-dwelling species (Table 5.8). Soutpansberg Peregrines took significantly more 'commuter species' (aerial insectivores, migrants or species which regularly commute between distant resources – e.g. sandgrouse, large columbids) than sympatric Lanners (76/318 or 23.9% *vs* 19/174 or 10.9% commuters respectively, $\chi^2_1 = 11.3$, $P<0.001$), but fewer overall than Cape Peninsula Peregrines (27.0 % *vs* 31.6% commuters respectively) and significantly fewer than Peregrines on the Orange River (110/407 or 27.0% *vs* 114/248 or 46.0% commuters respectively, $\chi^2_1 = 23.7$, $P<0.001$).

Discussion

Peregrine diet during the breeding season

As suggested by previous authors (Hustler 1983, Tarboton 1984, Mendelsohn 1988), columbids, and particularly *Streptopelia* doves, appear to be the staple food of Peregrines in southern Africa (Appendix 6, Tables 5.2 & 5.3). A similar preference for columbiforms applies to most other areas of the falcon's distribution where pigeons and doves are available as

***Table 5.6** Passage rates for the ten most numerous species recorded in 60 min point-counts conducted at falcon nest sites on the Cape Peninsula and in the Soutpansberg. Data provided are the percentage of the total sample of counts in which each species was recorded at least once, the average number and accumulated biomass of individuals recorded per count, and the average incidence per count of groups or individuals of each species*

species	% of counts	number of individuals	biomass (g)	incidence
Cape Peninsula (*n* = 64 counts)				
Feral Pigeon	14.1	0.6	195	0.5
Rock Pigeon	71.9	3.9	1345	2.3
Cape Turtle Dove	6.3	0.1	19	0.1
Black Swift	40.6	9.8	439	1.7
Alpine Swift	32.8	3.9	301	1.4
swift spp.	57.8	87.8	5356	6.6
Rock Martin	18.8	0.8	18	0.3
European Starling	7.8	0.9	71	0.8
Redwinged Starling	64.1	5.5	736	3.1
canary spp.	12.5	0.5	8	0.3
Soutpansberg (*n* = 114 counts)				
Rock Pigeon	18.4	0.6	198	0.3
Rameron Pigeon	5.3	0.1	58	0.1
Black Swift	33.3	14.3	642	2.4
Alpine Swift	59.6	12.0	923	3.4
swift spp.	52.6	75.5	4604	5.7
Rock Martin	51.8	10.2	225	3.9
Redwinged Starling	38.6	3.0	406	1.2
Blackeyed Bulbul	27.2	0.7	27	0.5
Cape Whiteye	10.5	0.2	2	0.1
sunbird spp.	12.3	0.2	2.5	0.2

prey (Cade 1982, Ratcliffe 1993). Small, aerially dextrous species such as swifts and bats appear more consistently in the diet of African Peregrines (Hustler 1983, Brown 1988, Mendelsohn 1988, this study) than has generally been reported for other populations. Conversely, large, terrestrial species such as anatids, galliforms and charadriiforms are less frequently taken in Africa than in other areas (e.g. Cade 1960, Porter & White 1973, Pruett-Jones et al. 1981, Mearns 1983, Ratcliffe 1993). These differences may partly reflect differences in prey availability, but can also be attributed to a greater tendency for African Peregrines (and perhaps other small, tropical forms of the species) to catch and kill prey in exclusively aerial strikes (Chapters 3 & 4).

Three *Streptopelia* dove species comprised nearly half (by frequency and mass) of the diet of Peregrines on the Cape Peninsula (Fig. 5.2, Appendix 6). British Peregrines are similarly specialized on large columbids (Mearns 1983, Ratcliffe 1993, Table 5.9). Typical of peri-urban Peregrine populations around the world (Cade & Bird 1990), Cape Peninsula pairs also took substantial numbers of commuting Feral or Domestic Pigeons and European Starlings, and occasionally preyed on escaped aviary birds (Appendix 6). Inexperienced, newly-fledged birds are particularly vulnerable to predation by raptors (Newton & Marquiss 1982, Rosenfield *et al.* 1995), and young doves and starlings were taken quite frequently by Cape Peninsula Peregrines. As observed in other temperate falcon populations (e.g. Newton *et al.* 1984, Parr 1985), juvenile birds became more prevalent in the diet as the breeding cycle progressed. This suggests that breeding by Peregrines on the Cape Peninsula may in part be timed to exploit the period of maximum productivity of their principal prey species (Jenkins 1991, Chapter 7).

Doves featured least prominently in the diet of Peregrines on the Orange River (Appendix 6, Tables 5.2 & 5.3); these were the most generalized feeders of the three Peregrine populations studied (Table 5.5). These falcons usually foraged in the river valley (Chapter 3), which was the focus of bird movements in the area. Aerial insectivores (swifts, hirundines and

Table 5.7 *Avian abundance and diversity in relation to habitat type in the Soutpansberg. Data provided are the average number of species, individuals and encounters recorded per 1 km line-transect, the average biomass of birds recorded per transect and the average perpendicular distance from the transect line at which sightings were made. Between nine and 12 transects were walked in each habitat*

habitat	number of species	number of individuals	biomass (g)	number of encounters	distance (m)
savanna woodland	6.7	21.6	1272	9.3	15
denuded woodland	5.6	30.4	805	9.8	18
forest & plantation	3.1	5.2	236	3.9	7
grassland & scrub forest	3.8	7.5	378	4.6	12
moist thornscrub	1.2	1.7	46	1.1	9
deciduous woodland	3.2	6.7	324	4.1	12
dry thornscrub	1.9	5.5	217	2.3	9

microchiropteran bats) and obligate drinkers (sandgrouse, columbids, granivorous passerines) were the groups most frequently taken, and were probably exposed to attack crossing rocky gorges or open stretches of the river, or travelling over arid flats adjacent to the floodplain. Namaqua Sandgrouse were uncommon in this area during the study period (pers. obs), but made up about 10% of individuals identified in Peregrine prey remains. Numbers of this nomadic species are likely to fluctuate annually (Maclean 1968). Given that collections of prey remains at Orange River nests were sporadic (Table 5.1), and often included old material accumulated over a number of breeding seasons, sandgrouse predation may have occurred in years before the study, when they were more plentiful in the area.

Soutpansberg Peregrines preyed on a wide variety of species (Appendix 6), most of which were secured in bird-rich woodlands at least 2 km from the base of the escarpment. Relatively fewer transient or commuter species, and more sedentary residents, were taken by these pairs than by Peregrines in the other two areas. However, the woodland species recorded as prey were generally those likely to fly furthest from, and highest

Table 5.8 *Foraging habitat use by breeding Peregrines and Lanners in the Soutpansberg, as inferred from the habitat affinities of prey species identified in food remains.* (A) *only includes prey species which were recorded in passage rate or line-transect counts (Table 7, Appendix 5).* (B) *combines the species in* (A) *with a number of important prey species which were not sighted on sample counts (e.g. Domestic Chicken, Namaqua Dove, Redfaced Mousebird,* Lamprotornis *starlings). Habitat preferences of species in (A) were determined from count data. The additional species in (B) were assigned to habitats on the basis of incidental observations in the area. Both comparative distributions are significantly different: (A) $\chi^2_6 = 12.6$, P = 0.049; (B) $\chi^2_6 = 79.7$, P<0.001*

favoured habitat of prey species	% frequency in Peregrine diet *(A)*	% frequency in Peregrine diet *(B)*	% frequency in Lanner diet *(A)*	% frequency in Lanner diet *(B)*
savanna woodland	26.7	39.0	19.0	19.5
denuded woodland	7.9	12.3	12.1	49.4
forest & plantation	0.3	0.3	-	-
grassland & scrub forest	5.4	5.4	1.4	1.4
moist thornscrub	-	-	-	-
deciduous woodland	0.3	0.3	1.4	1.4
dry thornscrub	0.3	0.3	-	-
cliffs	9.1	9.1	5.2	5.2

Table 5.9 Indices of diet breadth of Peregrines in other parts of the world, and measures of diet overlap between Peregrines and sympatric congeners

study population	number of taxa used	number of taxa >3%	diet breadth (B_A)
southern Scotland[a]	90	5	0.04
Victoria, Australia[b]	77	6	0.12
West Greenland[c]	11	6	0.24
Yukon River, Alaska[d]	29	8	0.41
sympatric Peregrines and Prairie Falcons *F. mexicanus*, Wasatch Mountains, Utah[e]			
Peregrines	33	9	0.31
Prairie Falcons	33	6	0.26
diet overlap: $C = 0.58$			
sympatric Peregrines and Gyrfalcons *F. rusticolus*, Colville River, Alaska[f]			
Peregrines	27	10	0.28
Gyrfalcons	27	5	0.09
diet overlap: $C = 0.42$			

food-niche parameters calculated using data from [a]Mearns 1983, [b]Pruett-Jones *et al.* 1981, [c]Rosenfield *et al.* 1995, [d]Hunter *et. al.* 1988, [e]Porter & White 1973, [f]Cade 1960

above, the protective canopy of the trees (e.g. Redfaced Mousebirds, *Lamprotornis* starlings). Mousebirds featured more prominently as Peregrine prey in the Soutpansberg than has been found in studies at other woodland sites, whereas rollers and woodpeckers were not taken (cf. Hustler 1983, Tarboton 1984), perhaps because they were less common in the environment. Francolins are among the largest species regularly taken by African Peregrines, and those recorded as prey of Soutpansberg Peregrines were probably all caught by females. These essentially terrestrial birds may have been caught in flight as they descended from the top of the cliff-line to the scree slopes below, as suggested by Hustler (1983).

Diet breadth indices calculated for South African Peregrines are comparable with equivalent data for populations in other areas (Table 5.9). These figures suggest that Peregrines in temperate areas – e.g. the Cape Peninsula (this study), southern Scotland (Mearns 1983), Victoria, Australia (Pruett-Jones *et al.* 1981) - are relatively specialized feeders.

Lanner Diet

Relatively small samples of identifiable prey remains were recovered from Lanner nest sites, perhaps because much of the prey they consumed was completely digestible. Also, Lanners in the Soutpansberg used smaller nest ledges than sympatric Peregrines (Chapter 2), reducing the space available for the accumulation of macro-remains, and increasing the need for nest hygiene and the active removal of uneaten prey.

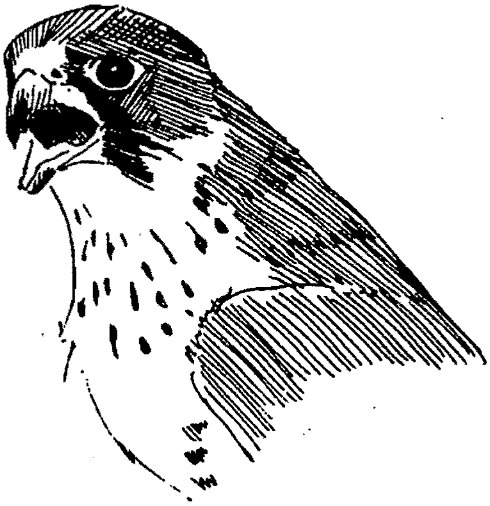
Few data are available on the diet of southern African Lanners. The only quantitative studies, based on small samples, suggest that phasianids (including domestic fowl) and columbids are important prey groups (Barbour 1971, Tarboton & Allan 1984, Kemp 1993). Lanners in the Soutpansberg were relatively specialized feeders, with young Domestic Chickens comprising nearly 40% of the prey recorded in remains (Appendix 6). Given the greater susceptibility of juvenile bones to damage and acid erosion, chickens may have been under-represented in these samples. Columbids were also important, and contributed more than phasianids to the biomass of identified prey (Table 5.4). Sources of free-range poultry were a considerable distance from most Lanner nest sites, and their frequency in prey remains suggests that Lanner hunting ranges extended well beyond those of nearby Peregrine pairs. One radio-tracked male Lanner foraged over rural settlement areas up to 10 km from the main escarpment (ARJ, unpublished data). Terrestrial or cursorial species predominated in the diet of Soutpansberg Lanners, and most prey were probably caught on or close to the ground.

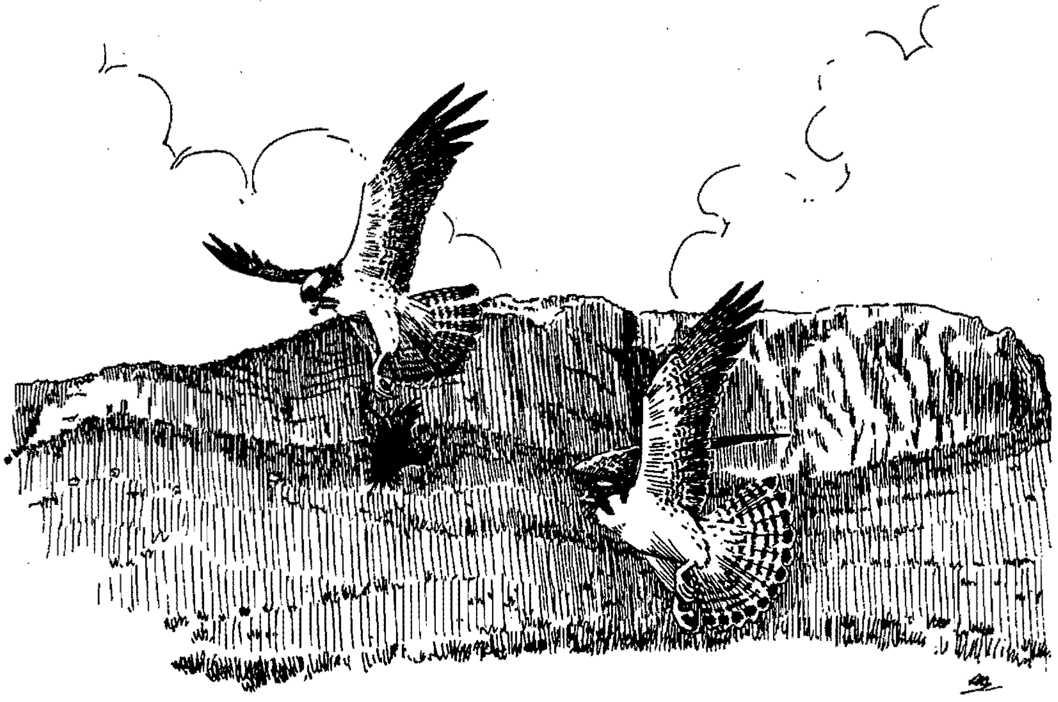
Perhaps contrary to expectations, Soutpansberg Lanners were more specialized feeders than sympatric Peregrines, both in terms of the taxonomic range of prey taken (Table 5.5) and the variety of foraging habitats used (Table 5.8). This result is consistent with other diet studies of Peregrines and sympatric congeners (Table 5.9), and probably reflects differences in the plasticity of foraging techniques. The Lanner's capacity to take prey in both aerial and ground strikes (Chapter 3) allowed exploitation of a locally abundant terrestrial prey base (free-range poultry) which was not available to the strictly aerial Peregrine. Hence, morphological and behavioural constraints may have forced Peregrines to take a wide variety of prey in a specialized manner, while Lanners, as more adaptable foragers, were able to specialize on fewer, perhaps more consistently profitable prey taxa. A similar contrast between diet breadth and foraging technique has been observed in sympatric shorebirds (Turpie & Hockey 1997).

Diet overlap and competition

Diet overlap between Soutpansberg Peregrines and Lanners (Table 5.5, Fig. 5.5) was moderate relative to those calculated using data from other studies of Peregrines and sympatric congeners (Table 5.9), and fell well below the suggested critical value for competing species of about 0.62 (Bosakowski & Smith 1992). Also, while competition theory predicts narrower food niches and reduced diet overlap between close pairs of competing species *versus* distant pairs (e.g. Nilsson 1984, Korpimäki 1987), the diet of falcon pairs in this study was not obviously affected by the presence of nearby pairs of congeners (e.g. Fig. 5.5). Hence, there was little to suggest active competition for food between Peregrines and Lanners in the Soutpansberg. Evidently, subtle differences in morphology, flying performance and hunting techniques of Peregrines and Lanners (Chapter 3) are sufficient to segregate foraging habitat and diet.

Acknowledgements – This study could not have been completed without the care, patience and skill of Graham Avery of the South African Museum, Cape Town, who identified all the avian prey remains. Margaret Avery identified the mammalian remains. Dave Allan kindly contributed prey remains collected at a Peregrine nest site in the Soutpansberg in 1988.





Chapter Six

Parental care at falcon nests in South Africa, and species- and area-specific differences in food availability

" ...a wild and adolescent creature whose father and mother in eagles' nests had fed him with bloody meat still quivering with life..." (T.H. White, The Goshawk, *Penguin Books 1975)*

Summary *– Parental care by Peregrines and Lanners during the nestling period was studied in two areas of South Africa. Comparisons were made between the quality of care administered to broods of Peregrines at nests in tropical (the Soutpansberg) and temperate (the Cape Peninsula) environments, and to broods of sympatric congeners in the tropics, to investigate postulated species- and area-specific differences in food availability. Time-lapse photography was used to measure provisioning rates and adult attendance at nests. In all three study populations, provisioning rates were largely dependent on brood size, and attendance was correlated with the age of young. The quality of parental care provided by Cape Peninsula Peregrines and Soutpansberg Lanners was superior (provisioning rates were over 20% higher and adults were more attentive at the nest) to that of Soutpansberg Peregrines. Direct observations and diet information from the analysis of prey remains suggested that female participation in the foraging effort was greatest at Peregrine nests in the Soutpansberg, which may have compromised nest security. The relatively poor quality of parental care by Peregrines in the Soutpansberg is symptomatic of food shortage for this specialist raptor in the tropics, in contrast to the more generalized Lanner.*

Introduction

The food requirements of breeding birds generally peak as young develop from hatchlings to fledglings (Skutch 1976, O'Connor 1984). In monogamous species with altricial or semi-altricial young, males usually provision the family for most of the nestling phase of the breeding cycle (Silver *et al.* 1985), while females remain at the nest to feed and protect the brood. Studies of breeding raptors have shown that nestling growth and mortality rates and post-fledging survival are influenced by the frequency of food deliveries to the nest (Newton 1978, 1979, Bortolotti 1986, Holthuijzen 1990) and the protection afforded the brood by attendant adults (Newton 1978, Ward & Kennedy 1996). Shortfalls in food supply may result in lower provisioning rates and increased provisioning effort, including greater participation by the female (Newton 1978, 1979, Rohner & Smith 1996), at the expense of nestling and adult condition (Dijkstra *et al.* 1990, Daan *et al.* 1996) and nest security (e.g. Ward & Kennedy 1996). Hence, levels of parental care are dependent on local environmental conditions, and are sensitive to fluctuations in prey availability (Newton 1979, Bortolotti 1986).

This chapter details provisioning and nest attendance by breeding Peregrines and Lanners in tropical South Africa, and by Peregrines in temperate South Africa. The quality of parental care observed is compared between similar, sympatric congeners and between conspecific populations. Differences may reflect species- or area-specific differences in prey availability (e.g. Poole 1982, Simmons 1986, Beissinger 1990) which are otherwise difficult to estimate, but which are likely to have a fundamental influence on the distribution, abundance and productivity of breeding pairs (Newton 1979, Simmons 1986, Jenkins 1991).

Methods

Research on the breeding behaviour of sympatric Peregrines and Lanners in the Soutpansberg was conducted over three seasons from 1991–1993, and comparative data were compiled for Peregrines on the Cape Peninsula from 1990–1995.

***Table 6.1** Details of time-lapse camera coverage and average provisioning and nest attendance figures (with ranges in parentheses) recorded at falcon nest sites on the Cape Peninsula and in the Soutpansberg in each year of the study*

site	year	brood size	age span (days)	days of coverage	number of feeds per day	nest attendance (% day)
Cape Peninsula Peregrines						
PA1	1990	3	9–17	6	8.8 (6–11)	69 (37–94)
	1991	3	17–26	7	7.7 (4–10)	19 (5–35)
	1992	3	17–24	7	8.6 (7–10)	13 (9–23)
	1995	4	14–25	10	8.8 (6–11)	51 (21–79)
PA2	1991	2	8–26	8	6.5 (5–8)	36 (5–98)
	1994	2	8–26	15	6.3 (4–9)	82 (45–98)
PA7	1990	3–2	1–26	24	6.1 (4–8)	62 (6–96)
	1992	3–2	4–20	13	6.6 (6–8)	53 (7–97)
	1993	2	9–15	5	5.6 (4–7)	87 (73–96)
PA8	1992	3–2	8–13	5	8.0 (7–9)	94 (84–97)
	1993	2	8–25	15	6.8 (5–9)	40 (9–97)
	1994	2	2–18	14	6.4 (4–9)	88 (27–98)
PA13	1994	3–2	9–17	7	7.1 (6–9)	59 (27–82)
Soutpansberg Peregrines						
PC1	1991	3	5–20	15	6.8 (4–11)	56 (9–97)
	1993	4–3	8–14	7	7.0 (4–9)	63 (25–89)
PC3	1991	3	6–10	5	6.2 (5–8)	33 (22–52)
	1992	3	9–15	8	6.9 (5–8)	23 (6–52)
	1993	3	5–18	12	5.9 (3–7)	34 (7–69)
PC5	1991	3	4–23	11	5.1 (2–11)	40 (7–94)
	1992	3	3–13	7	5.7 (4–8)	62 (7–96)
	1993	1	20–25	6	3.8 (2–5)	31 (9–51)
PC4	1993	3	6–25	12	5.8 (4–8)	41 (6–96)
Soutpansberg Lanners						
LC2	1993	3	4–12	9	9.2 (7–11)	54 (19–89)
LC3	1991	2	4–28	17	6.2 (4–8)	37 (4–98)
	1992	2	6–29	16	7.4 (3–11)	65 (11–93)
	1993	2	6–25	17	7.1 (4–9)	59 (12–96)
LC5	1992	5–4	5–23	18	7.4 (5–9)	17 (4–72)
LC6	1992	4	11–29	13	9.6 (7–12)	59 (12–96)
LC7	1991	4	3–22	17	10.4 (6–16)	43 (9–93)
LC8	1991	3	6–14	9	5.4 (2–8)	74 (25–100)
	1993	1	9–14	6	4.7 (3–6)	32 (25–39)

Measuring parental care

Most information on parental care at nests was gathered using time-lapse photography, which allowed the simultaneous collection of data at more than one remote, high-cliff site, over long periods, with minimum disturbance of breeding birds (Enderson *et al.* 1972). The time-lapse camera devices used in this study were constructed according to designs in Temple (1972), Enderson *et al.* (1972), and Davies (1994). Super-8 mm movie cameras, circuitry and power sources were contained in inconspicuous, weather-proof housings and positioned securely at active nests, overlooking the nest scrape and the brood of young, at distances of about 2–4 m. Each 5 min super-8 mm film comprises about 3600 frames. The frame interval of the time-lapse circuit was pre-set to expose a single frame every 92–192 s. A light-sensitive resistor deactivated the cameras overnight, so each film sampled activities at the nest over a period of 6–16 d, depending on local day-length and the time-lapse interval setting. Up to three films were exposed per monitored breeding attempt.

The films were analysed using a Super-8 mm viewer/editor, or a modified binocular dissecting microscope. Camera footage was converted to time-activity budgets by multiplying the number of sequential frames depicting an activity by the frame interval of the circuit. The time of day at which activities were recorded was estimated in terms of the time elapsed (number of frames exposed) since first light (about 06h00 in the Soutpansberg and about 05h00 on the Cape Peninsula). Adults photographed at the nest were sexed on the basis of size (females are obviously larger) and plumage (males are more contrastingly coloured). Four parental activity categories were distinguishable in the films: absent (neither adult present in the camera frame), present (standing on or perched close to the nest ledge but not in contact with the brood), brooding (covering or sheltering the brood) and feeding (distributing food to the nestlings, excluding occasions when adults fed themselves at the nest ledge). Seven parameters were derived from these basic categories, which collectively describe the quality of parental care observed at falcon nests each day. Other, independent variables recorded daily were brood size (number of young) and age of young (days since hatching), the frame interval of the time-lapse circuit (which was assumed to remain constant for the duration of each film), maximum and minimum temperatures, rainfall and wind velocity at 14h00. Nestling age was an average for each brood, calculated from an average hatch date based on direct observations of hatching clutches or estimated according to the onset of nestling provisioning. Each site was visited soon after hatching, and hatch date estimates were sometimes modified according to the overall stage of development of the brood. Age estimates were considered accurate to within 3–4 days. Meteorological data for each site were obtained from the nearest South African Weather Bureau weather station.

Direct observations were accumulated opportunistically at active sites in each population to test the efficiency of the time-lapse cameras and to provide data on the activities of breeding adults away from the nest ledge. Observations were made using 10x40 binoculars or a 20–60x spotting scope, from vantage points 200–400 m from the nest cliff. Full-day watches, each covering all the daylight hours in a 24 h cycle, were conducted at five different Peregrine sites on the Cape Peninsula and at four Peregrine sites and four Lanner sites in the Soutpansberg. The average duration of day watches was 14.6 h on the Cape Peninsula (range 14.3–15.0 h), 12.4 h at Peregrine sites in the Soutpansberg (range 12.0–12.6 h) and 11.9 h at Lanner sites in the Soutpansberg (range 11.4–12.0 h) – figures within the range of day

***Table 6.2** Results of stepwise regression analyses on parental care data recorded by time-lapse photography. The primary independent variable, the nature of its effect (positive or negative) and the percentage of the variation for which it accounts is indicated for each dependent variable. Age of young (A) or brood size (B) were the independent parameters selected first in all cases. All regressions were highly statistically significant (*P<0.001*)*

	Cape Peninsula Peregrines (*n* = 136 days)	Soutpansberg Peregrines (*n* = 83 days)	Soutpansberg Lanners (*n* = 122 days)
number of feeds per day	B + (19%)	B + (12%)	B + (20%)
number of feeds per hour	B + (25%)	B + (12%)	B + (18%)
average feed interval (min)	B - (21%)	B - (11%)	B - (17%)
time feeding per day (min)	B + (11%)	B + (26%)	B + (18%)
average time per feed (min)	A - (16%)	A - (14%)	A - (25%)
time brooding (% day)	A - (69%)	A - (48%)	A - (57%)
nest attendance (% day)	A - (73%)	A - (36%)	A - (38%)

lengths recorded by time-lapse cameras. Incidental observations at active sites (Cape Peninsula n = 343 observation periods, 560 h, Soutpansberg Peregrines n = 73 observation periods, 225 h, Soutpansberg Lanners n = 78 observation periods, 206 h) provided measures of hunting rates and the frequency of interspecific aggressive incidents in the vicinity of the nest cliff.

Rudimentary data were collected on nestling growth rates up to the age of about 30 days, when growth was essentially linear (e.g. Poole 1982). Nestlings at most camera-monitored sites were weighed to the nearest 5–10 g every 7–14 days, using 200 g or 1000 g spring scales. No allowance was made for crop contents, so absolute mass figures may be unreliable but

Table 6.3 *Mean weather conditions (with ranges in parentheses) during camera-monitored days, and correlation coefficients between climate and parental care at falcon nest sites (significant relationships are indicated* * $P<0.05$, ** $P<0.01$, *** $P<0.001$)

	max. temp. (°C)	min. temp. (°C)	rain (mm)	wind (ms^{-1})
Cape Peninsula Peregrines	23 (15–37)	13 (5–19)	1 (0–15)	8 (0–20)
Soutpansberg Peregrines	29 (18–37)	14 (8–19)	1 (0–17)	2 (0–7)
Soutpansberg Lanners	28 (16–35)	12 (3–21)	0 (-)	2 (0–7)
number of feeds per day				
Cape Peninsula Peregrines	-0.098	-0.150	-0.060	0.132
Soutpansberg Peregrines	0.208	0.036	-0.168	0.139
Soutpansberg Lanners	-0.034	0.174	-0.073	0.040
number of feeds per hour				
Cape Peninsula Peregrines	-0.108	-0.244**	-0.061	0.087
Soutpansberg Peregrines	0.171	0.023	-0.135	0.117
Soutpansberg Lanners	-0.109	0.195*	-0.058	0.033
average feed interval (min)				
Cape Peninsula Peregrines	-0.030	-0.100	-0.093	-0.207*
Soutpansberg Peregrines	0.312**	0.080	-0.087	-0.094
Soutpansberg Lanners	0.343***	0.189*	0.011	-0.097
time feeding per day (min)				
Cape Peninsula Peregrines	0.268***	0.081	-0.08	0.047
Soutpansberg Peregrines	-0.075	0.123	0.022	-0.086
Soutpansberg Lanners	0.018	-0.169	0.075	-0.020
average time per feed (min)				
Cape Peninsula Peregrines	0.054	0.259**	0.068	-0.030
Soutpansberg Peregrines	0.151	0.107	0.205	-0.019
Soutpansberg Lanners	0.085	-0.143	0.020	0.002
time brooding (% day)				
Cape Peninsula Peregrines	-0.008	0.128	0.074	0.138
Soutpansberg Peregrines	-0.403***	-0.231*	0.277*	0.132
Soutpansberg Lanners	-0.260**	-0.358***	0.041	-0.021
nest attendance (% day)				
Cape Peninsula Peregrines	0.069	0.092	0.073	0.199*
Soutpansberg Peregrines	-0.456***	-0.100	0.259*	0.124
Soutpansberg Lanners	-0.268**	-0.214	0.022	0.044

comparisons between populations are probably valid. Nestlings were only sexable at the age of 15–20 days, when dimorphism in mass and foot-size (Chapter 3) became evident. Once a brood had been sexed, this sex ratio was applied to earlier weighings of the same brood, assuming that females were the heavier individuals throughout.

Diet

Most prey delivered to nest sites had been plucked and sometimes partially eaten, so information on the identity and size of prey photographed by time-lapse cameras was unreliable. Prey remains (uneaten macro-remains, regurgitated pellets and plucked feathers) were collected regularly at most sites where cameras were operational, and provided a more accurate assessment of diet. Methods used in the preparation and analysis of prey remains and overall assessments of diet in each falcon population are detailed in Chapter 5.

Statistical analyses

Parental care data for each site were log-transformed to improve normality, and pooled within each population. Exploratory correlation and stepwise regression analyses were used to identify the independent variables which accounted for most of the variation in provisioning and nest attendance figures in each population. Means for each dependent variable were then compared within areas, between years, using a one-way analysis of covariance (ANCOVA) which allowed for the influence of independent covariates. Data for all years were then pooled, and ANCOVA was used to generate adjusted, comparable means for each of the three populations. ANCOVA requires equality of the covariate regression slopes for legitimate comparisons of adjusted means (Dixon *et al.* 1990). For variables where this assumption was not met, data for broods of the same size and similar ages were compared using non-parametric Mann-Whitney tests. Differences in nestling growth rates were examined using an analysis of linear regression by groups (Dixon *et al.* 1990). Prey remains were pooled within each population. Non-parametric, Kruskal-Wallis one-way analysis of variance (ANOVA) was used to test for differences in the mean weight of identified prey between years within populations, and between populations.

Results

Time-lapse data

A total of 136 complete days of camera coverage was obtained from five different Peregrine nests on the Cape Peninsula, 83 days of coverage were obtained from four Peregrine nests in the Soutpansberg, and 122 days were completed at six Soutpansberg Lanner nests (Table 6.1). Brood sizes varied from 2–4, 1–4 and 1–5 and the ages of young ranged from 1–26, 3–25 and 3–29 days respectively (Table 6.1). Once nestlings started to move actively around the nest ledge they spent considerable periods out of camera view, and no usable time-lapse data were obtained for broods older than about four weeks. On average, cameras operated for 13.9 h per day at Peregrine nests on the Cape Peninsula (range

Table 6.4 *Overall provisioning data (mean ± SD) from time-lapse camera coverage at falcon nest sites. Statistics in parentheses compare means for Peregrines on the Cape Peninsula or Lanners in the Soutpansberg with corresponding values for Soutpansberg Peregrines (n.s. = not significant, *P<0.05, **P<0.01, ***P<0.001)*

	Cape Peninsula Peregrines (n = 136 days)	Soutpansberg Peregrines (n = 83 days)	Soutpansberg Lanners (n = 122 days)
number of feeds per day	7.1 ± 2.0 (t_a = 6.09***)	5.6 ± 1.6	7.2 ± 1.9 (t_a = 6.41***)
number of feeds per hour	0.52 ± 0.14 (t_a = 2.10*)	0.48 ± 0.14	0.63 ± 0.15 (t_a = 7.30***)
average feed interval (min)	100 ± 28 (t_a = 1.62 n.s.)	107 ± 29	83 ± 23 (t_a = 6.65***)
average time per feed (min)	8.9 ± 2.4 (t_b = 1.58 n.s.)	8.4 ± 2.3	6.7 ± 1.8 (t_b = 6.07***)

t_a values from ANCOVA, means and standard deviations adjusted for the effects of brood size
t_b values from ANCOVA, means and standard deviations adjusted for the effects of age of young

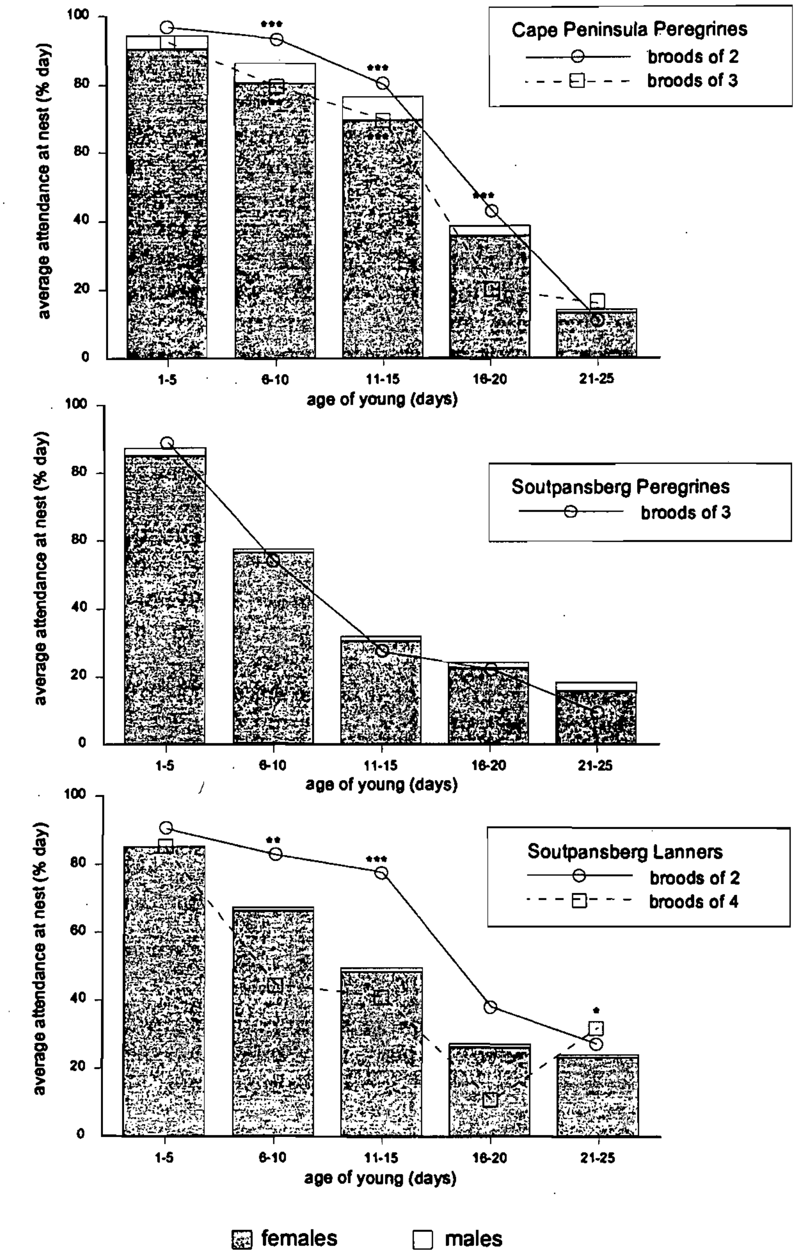


Figure 6.1 Time spent tending young at the nest by parent falcons. The bars show average daily nest attendance by males and females separately, for all broods, in relation to nestling age. The lines show attendance by both sexes combined, for different brood sizes, in relation to nestling age. Sample sizes (days of time-lapse camera coverage for each age and brood size category) are given in Table 6.5. Significant differences in attendance are indicated between Cape Peninsula Peregrines and Soutpansberg Peregrines, and between Soutpansberg Lanners and Soutpansberg Peregrines (Mann-Whitney tests; *P<*0.05,* **P<0.01, ****P<*0.001).*

10.6–15.5 h), 12.0 h per day at Peregrine nests in the Soutpansberg (range 9.6–13.1 h), and 11.7 h per day at Lanner nests in the Soutpansberg (range 9.6–13.1 h).

Within each sample, variation in parameters pertaining to feeding frequency was largely attributable to variation in brood size (provisioning rate increased with brood size), while variables describing nest attendance were strongly influenced by nestling age (attendance decreased with age of young) (Table 6.2). Climate was a secondary component of variation in parental care. Overall, weather conditions during camera-monitored days in the two study areas were not substantially different. The Cape Peninsula featured cooler maximum temperatures and stronger winds than the Soutpansberg (Table 6.3), and Soutpansberg Lanners experienced cooler, drier conditions than sympatric Peregrines (Table 6.3) because they started breeding earlier in the season. Correlations between weather and parental care at falcon nests (Table 6.3) may have been masked or exaggerated by the simultaneous progression of the breeding cycle (with coincident changes in the requirements of developing young) and seasonal climate changes. Ambient temperature was negatively correlated with feeding rates by Cape Peninsula Peregrines, and with brooding by both falcon species in the Soutpansberg (Table 6.3). Rainfall had a uniformly negative effect, and wind a positive effect on falcon provisioning, but neither relationship was statistically significant (Table 6.3). Per nestling provisioning rates by Peregrines tended to be higher on particularly windy days (Cape Peninsula n = 4 days, average = 3.50 feeds per nestling per day; Soutpansberg n = 8 days, average = 2.37 feeds per nestling per day) than on calm days (Cape Peninsula n = 35 days, average = 2.85 feeds per nestling per day; Soutpansberg n = 60 days, average = 2.05 feeds per nestling per day).

Provisioning rates by Soutpansberg Peregrines were significantly lower than those by Peregrines on the Cape Peninsula or Lanners in the Soutpansberg (Table 6.4), although feeds by Lanners were significantly shorter. Females were responsible for most of the parental duties at the nest in all three populations (Fig. 6.1) (cf. Enderson *et al.* 1972, Carlier 1993), including, on average, 94% of the daily feeds by Cape Peninsula Peregrines and 95% of the feeds by Soutpansberg Peregrines and Lanners. Adult Peregrines in the Soutpansberg generally spent less time tending their young than sympatric Lanners or Peregrines on the Cape Peninsula (Fig. 6.1). Although, within each population, larger broods were fed more and brooded less than smaller broods (Table 6.5), broods of two Peregrines on the Cape Peninsula were fed more than broods of three in the Soutpansberg, and Soutpansberg Lanners with four young were as attentive at the nest as nearby Peregrine pairs raising broods of three (Table 6.5). Allowing for differences in brood size (and hence brooding requirements), the brooding schedules of parent falcons in the three study populations were similar (Table 6.5), with regular daytime brooding maintained until the nestlings were about 15 days old (cf. Hovis *et al.* 1985). Daily nest attendance by Soutpansberg Peregrines dropped sharply from about 90% in the first five days after hatching to less than 40% between days 11–15, whereas Peregrine nestlings on the Cape Peninsula benefitted from the care and protection of their parents for at least 75–85% of the day until they were over two weeks old (Fig. 6.1).

The distribution of feeds in relation to time of day (Fig. 6.2) did not differ significantly between the two Peregrine populations ($\chi^2_3 = 6.04$, $P = 0.11$) or between Peregrines and Lanners in the Soutpansberg ($\chi^2_3 = 4.19$, $P = 0.24$). However, Peregrines in both areas had provisioning peaks in the early morning and late afternoon, which contrasted with the fairly even distribution of feeds through the day by Soutpansberg Lanners (Fig. 6.2).

Observations of breeding pairs

Because sample sizes were small and brood size and age varied considerably both within and between the

***Table 6.5** Average times invested daily by parent falcons in feeding and brooding their young, in relation to brood size and age. Significant differences between Cape Peninsula Peregrines or Soutpansberg Lanners and Soutpansberg Peregrines are indicated (Mann-Whitney tests; *P<0.05, **P<0.01, ***P<0.001)*

	brood size	age of young (days)				
		1–5	6–10	11–15	16–20	21–25
time feeding per day (min)						
Cape Peninsula Peregrines	2[a]	64	61	60*	55	51
	3[b]	54	66*	80***	64	71
Soutpansberg Peregrines	3[c]	62	58	52	57	49
Soutpansberg Lanners	2[d]	47	50	44	43	29**
	4[e]	73	71	58	61	52
time brooding (% day)						
Cape Peninsula Peregrines	2	84	81***	56***	27*	1
	3	84	62	26	1	1
Soutpansberg Peregrines	3	78	43	13	10	0
Soutpansberg Lanners	2	77	68*	57***	13	4
	4	75	24	16	2	6

sample sizes for each age class respectively: [a]n = 5, 13, 32, 18, 14 days; [b]n = 5, 13, 8, 10, 6 days; [c]n = 7, 28, 23, 9, 5 days; [d]n = 2, 15, 7, 12, 9 days; [e]n = 3, 8, 11, 10, 9 days

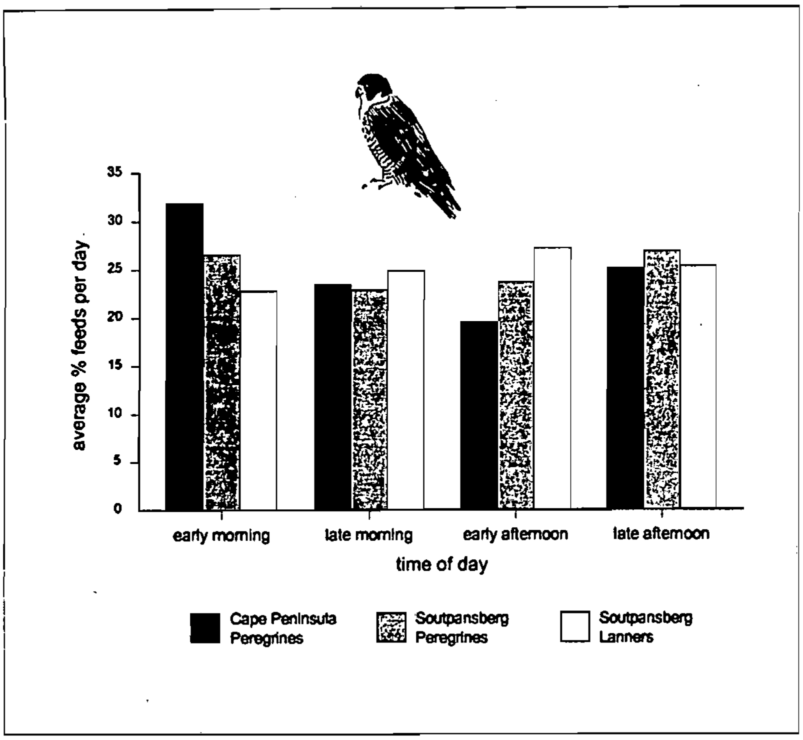


Figure 6.2 Food deliveries by falcons in relation to time of day. Cape Peninsula Peregrines n = *136 days, 942 feeds, Soutpansberg Peregrines* n = *83 days, 497 feeds, Soutpansberg Lanners* n = *122 days, 940 feeds.*

three samples (Table 6.6), data from day watches were not subjected to statistical analysis. However, these observations support the findings of the time-lapse study, with Cape Peninsula Peregrines and Soutpansberg Lanners achieving higher provisioning rates and maintaining greater parental attendance at the nest cliff than Soutpansberg Peregrine pairs (Table 6.6). Feeds observed at falcon nests where time-lapse cameras were in operation were all recorded by the cameras. Degrees of error in time-lapse estimates of the time of day and duration of these feeds generally were small, and were comparable between the three populations (Table 6.7). Overall, time-lapse cameras provided adequate records of provisioning and parental behaviour at falcon nests for a comparative study of this kind (also see Enderson *et al.* 1972, Hovis *et al.* 1985, Poole 1988).

Cape Peninsula Peregrines apparently enjoyed better local foraging conditions, and made significantly more hunts from the nest cliff (average hunting rate = 0.33 hunts per hour of observation) than Soutpansberg

Table 6.6 *Provisioning rates and parental attendance at the nest cliff recorded during day watches at falcon nest sites. Data are averages with ranges in parentheses*

	Cape Peninsula Peregrines (*n* = 6 days)	Soutpansberg Peregrines (*n* = 7 days)	Soutpansberg Lanners (*n* = 5 days)
brood size	2 (2–3)	3 (1–4)	3 (2–4)
age of young (days)	22 (10–38)	14 (6–21)	23 (17–31)
number of feeds per day	7.7 (6–10)	6.6 (4–10)	8.8 (6–10)
duration of feeds (min)	7.8 (6–10.7)	8.0 (7–9.4)	7.4 (4.6–10.9)
female attendance (% day)	87 (85–96)	74 (50–98)	79 (61–91)
male attendance (% day)	49 (28–77)	17 (2–21)	28 (21–40)

Table 6.7 Sampling error of time-lapse cameras in terms of the difference between the time of day and duration of feeds recorded by cameras at falcon nest sites and times recorded simultaneously by direct observation. Data provided are means ± SD, with ranges in parentheses

	Cape Peninsula Peregrines (*n* = 23 feeds)	Soutpansberg Peregrines (*n* = 9 feeds)	Soutpansberg Lanners (*n* = 22 feeds)
error in time of day of feed	35 ± 16	25 ± 37	18 ± 16
(min)	(8–75)	(3–121)	(0–78)
error in duration of feed	1.5 ± 1.7	1.1 ± 1.6	1.6 ± 2.1
(min)	(0.0–8.3)	(0.0–5.1)	(0.3–10.4)

Peregrines (average = 0.06 hunts per hour, Mann-Whitney $Z = 2.54$, $P = 0.01$). No successful strikes were observed at Soutpansberg Peregrine sites. Hunting rates at Soutpansberg Peregrine and Lanner sites were the same (Lanners average = 0.06 hunts per hour, $Z = 0.48$, $P = 0.63$). The threat of nest predation may have been lower on the Cape Peninsula, where Peregrine pairs defended their territories against large raptors and corvids significantly less often (average frequency of interspecific aggression = 0.17 incidents per hour of observation) than Soutpansberg Peregrine pairs (average = 0.30 incidents per hour, $Z = 4.32$, $P < 0.001$). Rates of interspecific aggression were similar for Soutpansberg Peregrines and Lanners (Lanners average

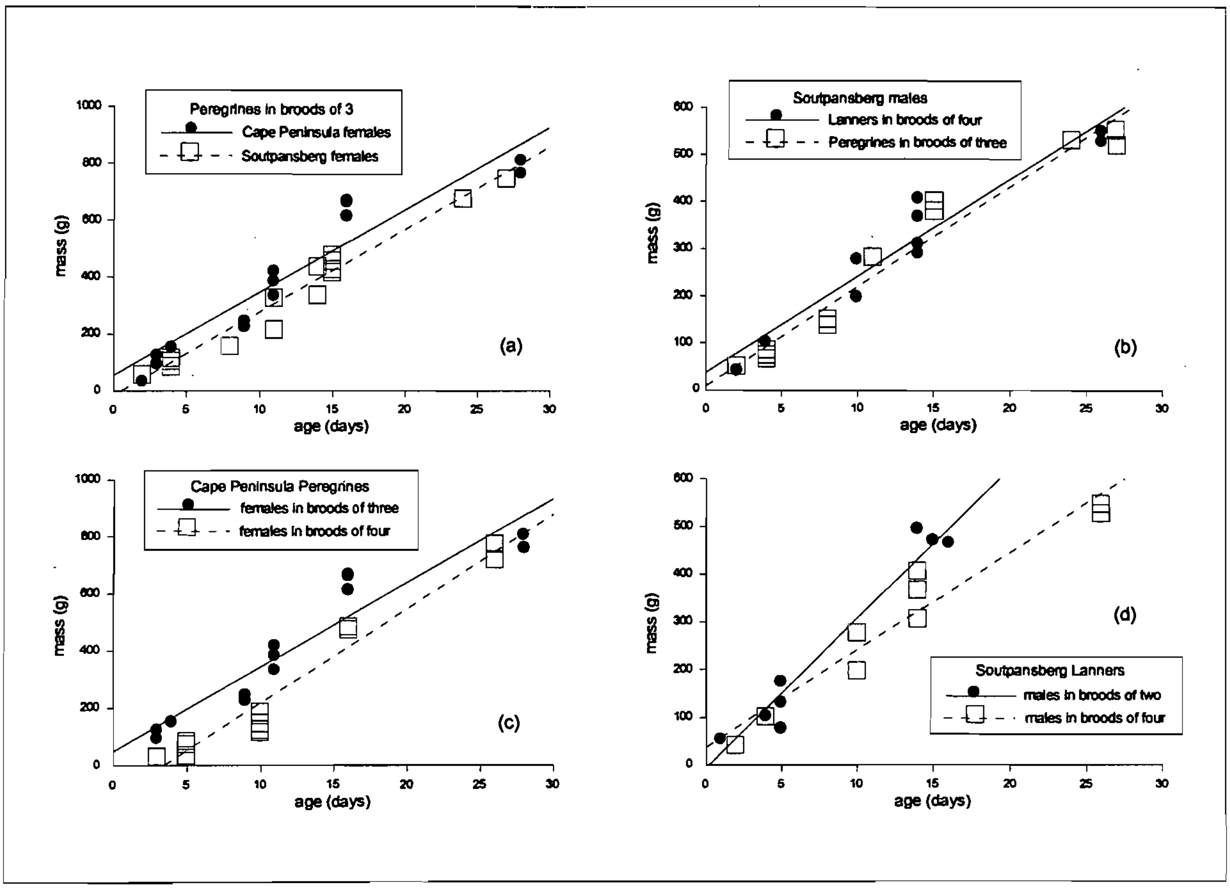


Figure 6.3 Selected comparisons of simplified nestling growth rates. The regression lines in (a), (c) and (d) are significantly different (ANOVA, $F_{2,27} = 4.4$, $P = 0.02$; $F_{2,26} = 11.2$, $P < 0.001$; $F_{2,14} = 10.6$, $P = 0.002$ respectively), while those in (b) are not ($F_{2,20} = 0.8$, $P = 0.48$).

***Table 6.8** The frequency of medium to large prey (>200 g), and the average mass of prey, identified in prey remains collected at camera-monitored falcon nest sites, in relation to brood size and age*

study population	brood size	age (days)	*n* prey individuals	% of prey >200 g	average mass of prey (g)
Cape Peninsula Peregrines	1–2	1–14	9	11.1	111
	1–2	15–42	94	18.1	127
	3–4	1–14	20	15.0	123
	3–4	15–42	19	21.1	129
Soutpansberg Peregrines	1–2	1–14	0	-	-
	1–2	15–42	13	7.7	104
	3–4	1–14	63	19.0	130
	3–4	15–42	79	29.1	148
Soutpansberg Lanners	1–2	1–14	8	0.0	71
	1–2	15–42	19	0.0	108
	3–4	1–14	23	4.3	121
	3–4	15–42	18	11.0	114

= 0.24 incidents per hour, $Z = 0.88$, $P = 0.38$).

Nestling growth rates

Insufficient data were collected for a rigorous analysis of nestling growth rates. Simple linear regressions were generated from the most substantial samples (Fig. 6.3). Statistical comparisons of these regression lines suggest that female Peregrine nestlings at sites on the Cape Peninsula generally were heavier than Soutpansberg females of the same age (Fig. 6.3a). Also, Soutpansberg Lanner males in broods of four grew at the same rate as Soutpansberg Peregrine males in broods of three (Fig. 6.3b), despite the tendency for young of both species to grow faster in smaller broods (Fig. 6.3c & d).

Diet at camera-monitored sites

The mean size (mass) of prey individuals identified in prey remains did not vary significantly within each falcon population between years (Kruskal-Wallis ANOVA, Cape Peninsula Peregrines $H = 1.84, P = 0.87$; Soutpansberg Peregrines $H = 2.84$, $P = 0.24$; Soutpansberg Lanners $H = 4.18, P = 0.12$), or between the three populations ($H = 0.32, P = 0.85$). The average size of prey delivered to the nest, and the incidence of medium to large prey in the diet, tended to increase with brood size and age in all three populations (Table 6.8). These trends probably correspond with increases in the female's contribution to provisioning (e.g. Newton 1978, Geer 1981), and were most pronounced at Soutpansberg Peregrine sites (Table 6.8).

In terms of the number of individuals identified in prey remains collected at camera-monitored nests, the diet of Peregrines on the Cape Peninsula comprised 44% *Streptopelia* doves and 13% *Columba* pigeons (= 57% columbids), 19% starlings, 11% swifts and 13% other birds, the diet of Soutpansberg Peregrines comprised 30% *Streptopelia* doves and 20% *Columba* pigeons (= 50% columbids), 11% mousebirds, 4% swifts and 35% other birds, and the diet of Soutpansberg Lanners comprised 21% *Streptopelia* doves and 3% *Columba* pigeons (= 24% columbids), 41% Domestic Chickens *Gallus gallus*, 9% plovers and 26% other birds. Juvenile birds made up 6% of the diet of Cape Peninsula Peregrines and 46% of the diet of Lanners in the Soutpansberg. No juvenile birds were recorded among the prey remains collected at Soutpansberg Peregrine sites.

Discussion

Feeding rates and time invested in brooding and guarding nestlings are fundamental elements of avian parental care (Skutch 1976, Simmons 1989). This study has demonstrated clear differences in these parameters between conspecific falcon populations in different environments, and between sympatric congeners.

Nestling physiology, climate and diet quality

The food requirements of nestlings in each of the three falcon populations may have varied according to differences in nestling physiology, which could account for observed discrepancies in feeding rates. Basal energy requirements of falconiforms correlate with body mass and climate (Wasser 1986). The fledging periods of South African Peregrines and Lanners are

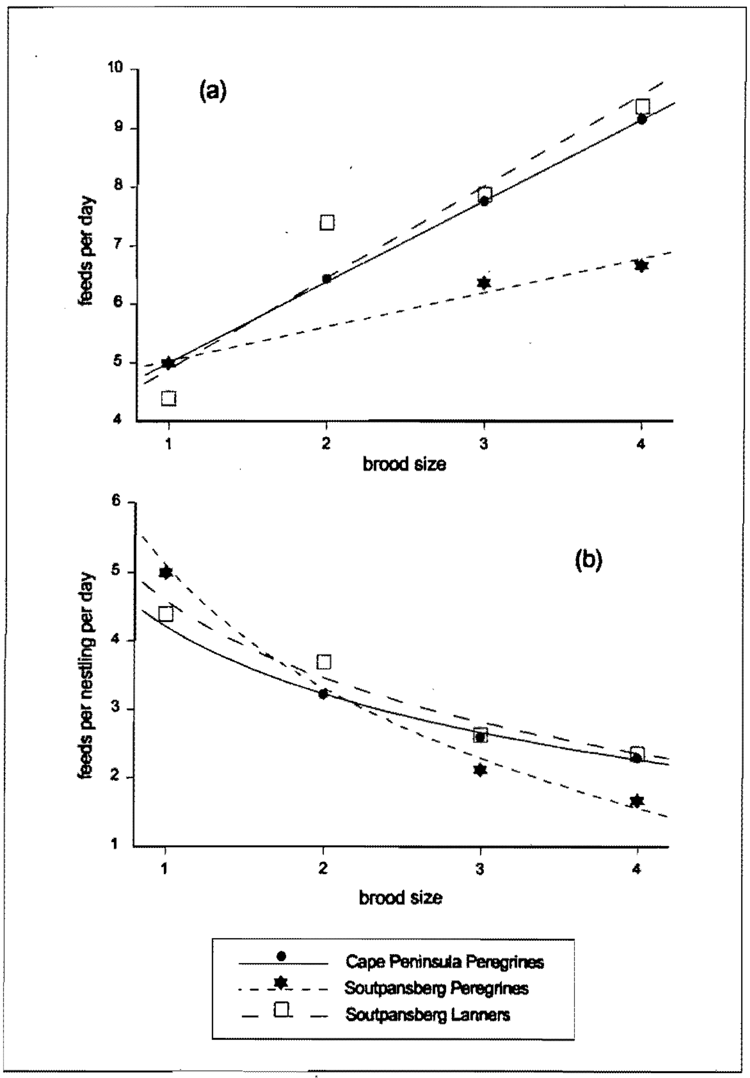


Figure 6.4 Provisioning rates by Peregrines and Lanners to broods aged 10–20 days. Correlation coefficients and slopes for the lines in (a) are: Cape Peninsula Peregrines $r^2 = 0.99$, *$b = 1.37$,* P = *0.01, Soutpansberg Peregrines* $r^2 =$ *0.97, $b = 0.58$,* P = *0.10, Soutpansberg Lanners* $r^2 = 0.91$, *$b = 1.54$,* $P<0.05$.

approximately the same (Steyn 1982, pers. obs) and adults are similar in mass (Chapter 3), so the resting metabolic rates of nestlings at the same stage of development probably do not differ under the same environmental conditions. Minor differences in the ambient temperatures experienced by each falcon population (Table 6.3) are unlikely to have affected nestling energetics, with extreme temperatures being moderated by brooding adults, sheltered nest ledges and the dampening effect of the nest cliff on temperature fluctuations (Williams 1984).

While Soutpansberg Peregrines and Lanners delivered similar sized prey, Lanners consumed each meal more rapidly (Table 6.4). This was probably because Lanners preyed heavily on juvenile chickens with a high ratio of edible to inedible tissue and bone, which can be broken up and distributed to nestlings more rapidly than adult wild birds of the same size. Phasianids yield relatively poor quality meat, containing about 10% less energy per unit mass than columbids and smaller birds (Barton & Houston 1993). Hence, Lanner provisioning rates in the Soutpansberg may have exceeded those of sympatric Peregrines to compensate for the inferior nutritional quality of their prey. Alternatively, the Lanner's ability to raise young on a chicken-based diet suggests a superior capacity to assimilate nutrients, given that Peregrines are unable to maintain condition on foods with low energy values (Barton & Houston 1993). As less specialized foragers than Peregrines (Chapters 3 & 4), Lanners may have longer intestines to increase digestive efficiency over a broader range of lower quality foods (Barton & Houston 1993).

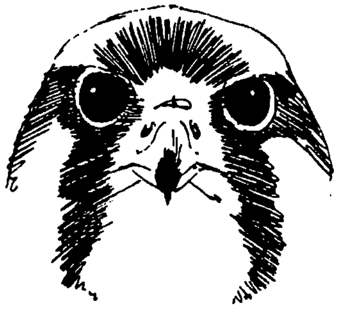
Parental care and food availability

Soutpansberg Peregrines provided their developing young with about 20% less food per day, and substantially less protection from adverse weather and predators, than either Cape Peninsula Peregrines or Soutpansberg Lanners. Given that the food and protective requirements of nestlings in the three populations were not substantially different, these contrasts in parental care profiles suggest area or species-specific differences in prey availability.

Newton (1978) ascribes the lack of effective partitioning of parental roles and a limited capacity to increase provisioning rates with nestling demands to poor food conditions for breeding raptors. Diet and nest attendance data presented here (Fig. 6.1, Table 6.8) indicate that female Peregrines in the Soutpansberg were forced to supplement the provisioning efforts of their mates relatively early in the breeding cycle. This, in turn, compromised their capacity to protect their young from predators – one brood was killed by a snake after a prolonged absence from the nest site by both adults (Jenkins 1994). Despite female contributions, Soutpansberg Peregrine provisioning rates were still inferior to those of Cape Peninsula pairs or Soutpansberg Lanners in terms of their capacity to increase feeding rates with brood size (Fig. 6.4).

Per capita provisioning rates have been correlated with nestling growth rates and breeding success in raptors (e.g. Poole 1982, Bortolotti 1986, Beissinger 1990, Dijkstra et al. 1990, Holthuijzen 1990). In this study, differences in provisioning rates were reflected to some extent in nestling growth rates (Fig. 6.3), and Soutpansberg Lanners raised more large broods than sympatric Peregrines (Table 6.1). However, Peregrine brood sizes were lower on the Cape Peninsula than in the Soutpansberg (Table 6.1), mostly because nestling mortality rates were (inexplicably) higher (see Chapter 7).

Previous experimental studies have suggested that tropical raptors are reproductively limited by food abundance, and breeding pairs achieve lower food delivery rates than pairs of the same or related species at higher latitudes (Poole 1982, Simmons 1986, Beissinger 1990). Data from tropical and temperate Peregrines in South Africa support this conclusion. The superior provisioning performance of Lanners over Peregrines in tropical South Africa can largely be explained by the Lanner's less specialized foraging mode and broader prey spectrum (Chapters 3–5).



Chapter Seven

Reproduction and factors affecting breeding success of Peregrines and Lanners in South Africa

"No place in the world knows of such storms as this Cape or promontory of Good Hope." (Johan Neuhof 1654, quoted by Jose Burman in The False Bay Story, *Human & Rousseau 1977)*

Summary *– Breeding success was recorded for three Peregrine populations in South Africa over nine years, and for Peregrine and Lanner populations in an area of sympatry over three years. The objectives of the study were to measure geographic and interspecific variation in reproductive performance, and determine environmental correlates of productivity. Territory occupancy, the frequency of breeding per occupied territory and clutch size did not vary significantly between the three Peregrine populations. Peregrine breeding success was lowest on the Cape Peninsula (1.11 young fledged per territorial pair), higher in the Soutpansberg (1.36) and highest on the Orange River (1.70). Fledging rates of Soutpansberg Peregrines and Lanners were not significantly different, although annual productivity of the Lanner population was consistently higher. Neither species' breeding success was significantly depressed by the presence of close neighbouring pairs of the other, suggesting that they were not active competitors. Breeding performance by Peregrines on the Cape Peninsula correlated strongly with spring weather conditions: egg and hatchling survival was lower in wet years, and fledging rates were higher in warm years. Annual productivity of Orange River Peregrines correlated positively with the height of the river at the onset of breeding, and productivity of Soutpansberg Peregrines was higher in seasons following years of high rainfall. Elements of the physical structure of the nesting habitat – exposure of the nest ledge, height of the nest cliff – correlated with Peregrine breeding performance. Breeding success of Soutpansberg Lanners was largely unaffected by any of the environmental variables considered. Overall, Peregrine productivity reflected fluctuations in the physical environment which themselves influenced prey availability.*

Introduction

Many of the larger members of the genus *Falco*, and in particular the Peregrine, have extensive distributions spanning wide ranges of biotic and abiotic conditions (Cade 1982, del Hoyo *et al.* 1994). Recognition and understanding of broad-scale patterns of abundance and productivity across these environmental spectra are constrained by practical considerations. Given the nature of these birds, surveys of density and breeding success over expanses of typically rugged terrain are labour intensive and often unreliable (Hickey 1969, Ratcliffe 1993), and options for experimental or manipulative research generally are limited. Long-term, intensive studies of focal populations are the main source of comparable data on productivity. Few such studies have been conducted on tropical or subtropical falcons (Cade 1982, Cade *et al.* 1988), and virtually no data of this kind are available for large falcons in the Afrotropics. This chapter details nest success and factors affecting breeding performance of Peregrine and Lanner populations in South Africa.

Methods

Peregrine breeding data were collected on the Cape Peninsula, the lower Orange River and in the Soutpansberg over nine seasons, from 1989–1997. Lanners were studied in the Soutpansberg from 1991–1993. Ground or aerial searches for falcon nest sites in these areas were conducted opportunistically through the study period. Each study area was surveyed completely at least once, but remote sections remained relatively unexplored and it is likely that some occupied territories were overlooked.

Breeding parameters

For comparative purposes, the nature and presentation of the breeding data collected, and much of the terminology used, follows Mearns & Newton (1988), Olsen & Olsen (1988, 1989a, 1989b) and studies in Cade *et al.* (1988). Thorough monitoring, with multiple visits to each territory through the season, was carried out on the Cape Peninsula in each year of the study, and in the Soutpansberg from 1991–1993. Otherwise, annual one-visit surveys provided rudimentary measures of breeding success of Peregrines in the Soutpansberg and on the Orange River.

Egg-laying dates were rarely recorded by direct observation. Most were estimated from the timing of behavioural changes associated with the onset or termination of incubation and/or by back-dating (subtracting 34 days for the egg-laying and incubation period – Olsen & Olsen 1989a, pers. obs) from hatching dates estimated according to nestling sizes and weights (Olsen & Olsen 1989a, Chapter 6). Complete assessments of breeding success at active sites involved at least three visits to the nest ledge itself, to determine clutch size, the number of young hatched from the clutch (brood size), and the number of young surviving to at least 25 days old (in the absence of information from later in the cycle, considered to be the number of young fledged). However, some ledges were inaccessible and it was not practical to visit others more than once in a season, so sample sizes vary within and between years. Young fledged per territorial pair was considered the best measure of breeding success (e.g. Mearns & Newton 1988), although young fledged per successful pair was emphasized if accurate counts of occupied territories or breeding pairs were unavailable. The productivity of each population was expressed in terms of the average number of young fledged per territorial pair per year.

The breeding success of pairs of Peregrines or Lanners in the Soutpansberg with close neighbouring pairs of congeners was compared with that of pairs which were distant from pairs of congeners (see Chapter 5 for details on the number and distribution of these sites). This provided a coarse test of the extent to which possible competition between the two species inhibited their performance.

Table 7.1 Territory occupancy and the frequency of breeding and successful breeding by Peregrines and Lanners in three areas of South Africa (all data pooled)

population	number of territorial pairs[a]	number of breeding pairs[b]	number of successful pairs[c]
Peregrines 1989–1997			
Cape Peninsula[d]	106 (96%)	72 (68%)	52 (49%)
Orange River	49 (85%)[e]	35 (71%)	35 (71%)
Soutpansberg	48 (86%)[e]	31 (65%)	28 (58%)
overall	201 (90%)[e]	136 (68%)	114 (57%)
Soutpanberg 1991–1993			
Peregrines	20 (95%)	16 (80%)	13 (65%)
Lanners	26 (96%)	23 (89%)	21 (81%)

[a] (% of surveyed territories)
[b] pairs which laid at least one egg (% of territorial pairs)
[c] pairs which fledged at least one young (% of territorial pairs)
[d] including two replacement clutches
[e] minimum figures based on one-visit surveys in some or all years

During the study, Peregrine nestlings were removed under permit from sites in each area (Cape Peninsula, two in 1991 and two in 1992; Orange River, two in 1991; Soutpansberg, two in 1990 and four in 1991) for the establishment of captive breeding facilities. Most of these birds were at least three weeks old when removed, and all were classed as fledged young in subsequent analyses of breeding success.

Environmental variables

Meteorological data were obtained from the South African Weather Bureau for the weather station nearest to each nest site. These data included mean daily maximum and minimum temperatures, total rainfall and number of days with >0.1 mm of rain, for the three months spanning the pre-laying to mid-nestling periods, and aggregate rainfall over the 12 months before each breeding season. Monthly aggregate volumes of waterflow at the Vioolsdrif gauging station (28°47'S, 17°38'E) on the lower Orange River were provided by the South African Department of Water Affairs and Forestry.

Variables describing the physical structure of the nesting habitat were measured for a subsample of breeding attempts (Chapter 2) and assessed as correlates of breeding success. The total exposure and floor area of the nest ledge and the vertical height of the nest cliff (see Appendix 2 for definitions of these variables) were considered likely to affect nestling thermal and spatial requirements and the risk of predation respectively (Chapter 2). Nest cliff height and the total elevation of the nest above the surrounding terrain may have influenced conditions for hunting and territory maintenance (Tarboton 1984, Mearns & Newton 1988, Chapters 2 & 4). Selected behavioural data were used as indices of environmental conditions. The frequency of hunts made in the vicinity of the nest during the breeding season (Chapter 4) was considered a possible

***Table 7.2** Laying dates and the duration of the laying season of Peregrines and Lanners in three areas of South Africa. For each study population, only years in which at least three laying dates were determined are shown*

population/ year	*n*	mean	earliest to latest	length (d)
Peregrines				
Cape Peninsula				
1990	4	22 September	10 September - 8 October	28
1991	3	25 September	15 September - 6 October	21
1992	4	30 September	16 September - 26 October	40
1993	4	18 September	2 September - 23 September	21
1994	11	4 October	7 September - 4 November	58
1995	7	16 September	27 August - 25 September	29
1996[a]	7	29 September	28 August - 18 October	51
1997	15	18 September	3 September - 7 October	34
Orange River				
1990	5	4 September	28 August - 18 September	21
1995	4	8 September	1 September - 14 September	13
1996	4	20 September	5 September - 4 October	29
Soutpansberg				
1991	6	26 August	20 August - 7 September	18
1992	4	31 August	24 August - 12 September	19
1993	5	25 August	14 August - 7 September	24
1995	3	19 August	5 August - 2 September	28
Lanners				
Soutpansberg				
1991	7	24 July	18 July - 5 August	18
1992	7	9 August	1 August - 25 August	24
1993	7	28 July	18 July - 7 August	20

[a]including laying dates for two replacement clutches

index of prey availability, while the frequency of interspecific aggression was used as an index of predation pressure and the frequency of intraspecific aggressive incidents was thought to reflect territorial pressure. These data were only included for sites with at least 10 h of observation time during a given breeding season.

Statistical analyses

Breeding data from each falcon population were pooled for all sites, in all years, and analysed and compared in terms of the total sample of occupied territories or breeding or successful pairs. Breeding performance was also examined in terms of the overall productivity of each population.

Data were log-transformed where necessary to improve normality. Depending on sample sizes available, one-way analysis of variance (ANOVA) and Student's *t* tests or non-parametric Kruskal-Wallis, Mann-Whitney and Wilcoxon paired-sample tests were used to determine the statistical significance of differences in breeding and other parameters between populations or within populations between years. Contingency tables and χ^2 (with Yates' correction for χ^2_1) were used to test for differences in frequency distributions. Specific categories with significantly different frequencies were identified by comparing adjusted residuals (Everitt 1977). Correlation matrices were generated to examine relationships between environmental variables and breeding success. Stepwise multiple regression analysis, conducted using BMDP software (BMDP Statistical Software. Inc., Los Angeles, California), was used to determine which combinations of environmental factors best explained variation in breeding performance.

Results

A maximum of 17 Peregrine territories were monitored annually on the Cape Peninsula, eight on the Orange River and seven Peregrine and nine Lanner territories in the Soutpansberg (Appendix 9). The number of known territories in each area increased through the study period (Appendix 9), partly because surveys became progressively more extensive and efficient and partly because new pairs took up residence at formerly unoccupied sites. Nearest neighbour distances between known Peregrine nest sites averaged 5.6 km on the Cape Peninsula (range = 1.3–18.0 km), 6.3 km on the Orange River (range = 2.3–11.3 km), and 9.7 km in the Soutpansberg (range = 3.5–17.0 km), while Soutpansberg Lanner sites averaged 5.2 km apart (range 1.3–14.5 km).

Peregrine breeding performance

The three Peregrine populations did not differ significantly in terms of the proportion of known territories occupied each year (Kruskal-Wallis, $H = 2.20$, $P = 0.33$), or the proportion of territorial pairs attempting to breed ($H = 0.87$, $P = 0.65$) or breeding successfully ($H = 3.80$, $P = 0.15$) (Table 7.1, Appendix 9). Peregrine fledging rates per territorial pair varied significantly between years on the Cape Peninsula (ANOVA, $F_{8,96} = 4.25$, $P = 0.002$) but not on the Orange River ($F_{8,38} = 1.51$, $P = 0.19$) or in the Soutpansberg ($F_{8,36} = 0.99$, $P = 0.46$). There was more variation in breeding success between sites in the Soutpansberg ($F_{6,38} = 2.81$, $P = 0.02$) than on the Cape Peninsula ($F_{16,88} = 1.74$, $P = 0.05$), while fledging rates did not vary significantly between sites on the Orange River ($F_{7,39} = 0.88$, $P = 0.53$).

All data pooled: Laying dates varied significantly between the three Peregrine populations ($F_{2,96} = 47.7$,

***Table 7.3** Overall breeding performance of Peregrines and Lanners in three areas of South Africa (all data pooled)*

population	clutch size (*n*)	brood size[a] (*n*)	number of young fledged per		
			successful pair (*n*)	breeding pair (*n*)	territorial pair (*n*)
Peregrines 1989–1997					
Cape Peninsula[b]	2.78 (51)	2.06 (53)	2.29 (51)	1.65 (71)	1.11 (105)
Orange River	-	-	2.42 (33)	2.42[c] (33)	1.70[c] (47)
Soutpansberg	3.14 (14)	2.71[c] (21)	2.44 (25)	2.18[c] (28)	1.36[c] (45)
overall	2.86 (65)	2.24[c] (74)	2.37 (109)	1.97[c] (132)	1.31[c] (197)
Soutpansberg 1991–1993					
Peregrines	3.00 (12)	2.69 (16)	2.42 (12)	1.93 (15)	1.53 (19)
Lanners	3.42 (12)	2.80 (20)	2.86 (21)	2.61 (23)	2.31 (26)

[a] per breeding pair
[b] including two replacement clutches
[c] maximum figures based on data from one-visit surveys in some or all years

Table 7.4 Frequency distributions of clutch and fledged brood sizes recorded at Peregrine and Lanner nests in three areas of South Africa

population	clutch					fledged broods				
	1	2	3	4	5	1	2	3	4	5
Peregrines 1989–1997										
Cape Peninsula[a]	4	13	24	9	0	7	25	14	4	0
Orange River	-	-	-	-	-	2	15	16	0	0
Soutpansberg	0	1	10	3	0	3	8	14	0	0
overall	4	14	34	13	0	12	49	44	4	0
Soutpansberg 1991–1993										
Peregrines	0	1	10	1	0	3	1	8	0	0
Lanners	1	1	3	6	1	1	7	7	6	0

[a]including two replacement clutches

$P<0.001$). On average, Soutpansberg pairs (mean laying date 25 August, $n = 26$) laid 16 days earlier than those on the Orange River (mean laying date 10 September, $n = 14$, Student's $t_{38} = 5.12$, $P<0.001$), and Orange River pairs laid 14 days earlier than those on the Cape Peninsula (mean laying date 24 September, $n = 56$, $t_{68} = 3.48$, $P<0.001$). The duration of the laying season did not vary significantly between areas ($H = 4.90$, $P = 0.09$), but was most variable between years on the Cape Peninsula (Table 7.2).

Peregrine clutch sizes on the Cape Peninsula and in the Soutpansberg were not significantly different (Table 7.3, $t_{63} = 1.49$, $P = 0.14$), and clutches of each size were recorded with equal frequency (Table 7.4, $\chi^2_3 = 3.80$, $P = 0.28$). However, broods hatched per breeding pair were significantly larger in the Soutpansberg (Table 7.3, $t_{72} = 2.22$, $P = 0.03$). Breeding success varied significantly between the three areas in terms of the number of young fledged per occupied territory (Table 7.3, $F_{2,194} = 3.45$, $P = 0.03$), but not in terms of young fledged per successful pair (Table 7.3, $F_{2,106} = 0.48$, $P = 0.62$). Fledged broods of each size occurred with similar frequency (Table 7.4, $\chi^2_6 = 10.92$, $P = 0.09$).

While few data were obtained on the incidence or causes of breeding failure in the Orange River or Soutpansberg populations, breeding success on the Cape Peninsula was affected by relatively high rates of egg or hatchling mortality. At least 27% of breeding attempts in this area failed during incubation or at hatching (Table 7.5). Of 142 eggs laid at Cape Peninsula sites and monitored throughout the breeding cycle, 29 (20.4%) failed during incubation, 33 (23.2%) died or disappeared soon after hatching, seven (4.9%) died or disappeared as nestlings and 73 (51.4%) produced fledged young. In contrast, of 37 eggs laid at Soutpansberg nests, failures at each stage numbered 2 (5.4%), 4 (10.8%) and 4 (10.8%) respectively, and 27 (73%) produced fledged young. These are significantly different distributions ($\chi^2_3 = 10.11$, $P = 0.02$), with a higher frequency of egg mortality (adjusted residual = 2.2, $P<0.05$) and lower fledging success per egg (adjusted residual = -2.4, $P<0.05$) on the Cape Peninsula.

Annual productivity: Mean annual productivity did not vary significantly between the three Peregrine populations (Appendix 10, $H = 3.95$, $P = 0.14$), but was lowest on the Cape Peninsula (1.04 young fledged per territorial pair per year), intermediate in the Soutpansberg (1.44) and highest on the Orange River (1.72).

Peregrines and Lanners in the Soutpansberg

Between 1991–1993, Soutpansberg Peregrines and Lanners did not differ significantly in the proportion of occupied to known territories (Mann-Whitney $Z = 0$, $P = 1.00$) or in the proportion of territorial pairs attempting to breed ($Z = 0.87$, $P = 0.38$) or breeding successfully ($Z = 0.89$, $P = 0.38$; Table 7.1, Appendix 9). Breeding success of Peregrines did not vary significantly between years ($F_{2,16} = 1.86$, $P = 0.19$) or between sites ($F_{6,12} = 1.50$, $P = 0.26$). Lanner fledging rates were not significantly different between years ($F_{2,23} = 0.06$, $P = 0.94$), but did vary between sites ($F_{8,17} = 2.66$, $P = 0.04$).

All data pooled: On average, Lanners (mean laying date 31 July, $n = 21$) laid 27 days earlier in the season than Peregrines (mean laying date 27 August, $n = 15$, $t_{34} = 8.65$, $P<0.001$), but the length of the laying season was the same (Table 7.2). Average clutch sizes ($t_{22} = 1.24$, $P = 0.23$) and brood sizes ($t_{34} = 0.29$, $P = 0.77$) per breeding pair were not significantly different (Table 7.3). Peregrines tended to lay more three-egg clutches and Lanners laid more clutches of four (Table 7.4, $\chi^2_4 = 9.34$, $P = 0.05$; Peregrines clutches of three, adjusted residual = 2.9, $P<0.001$; Lanners clutches of four, adjusted residual = 2.2, $P<0.05$). The average number

***Table 7.5** Account of complete breeding failures by Peregrines and Lanners in three areas of South Africa (all data pooled)*

population	cause of failure	% of breeding attempts	% of occupied territories
Peregrines 1989–1997			
Cape Peninsula[a]	non-laying	-	32
	clutch addled or broken	6	4
	clutch disappeared	1	1
	clutch abandoned	6	4
	young disappeared at hatching	14	9
	young disappeared	1	1
Orange River	non-laying	-	29
Soutpansberg	non-laying	-	36
	young disappeared	6	4
	young taken by predators	3	2
Soutpansberg 1991–1993			
Peregrines	non-laying	-	20
	young disappeared	13	10
	young taken by predators	6	5
Lanners	non-laying	-	11
	clutch addled or broken	9	8

[a] including two replacement clutches

of young raised per territorial pair of each species was not significantly different (Table 7.3, t_{43} = 1.85, P = 0.07), although Lanners raised large broods relatively more frequently (Table 7.4, χ^2_3 = 9.84, P = 0.02, adjusted residual for fledged broods of four = 2.0, P<0.05). Average fledging rates of Peregrine and Lanner pairs with close neighbouring pairs of congeners were not significantly lower than those of pairs with distant neighbouring pairs of congeners (Peregrines 1.12 young fledged per territorial pair (n = 8) *vs* 1.82 (n = 11), Z = 1.14, P = 0.25; Lanners 1.92 (n = 12) *vs* 2.64 (n = 14), Z = 1.66, P = 0.09).

Annual productivity: The productivity of Peregrines in the Soutpansberg from 1991–1993 was lower than that of sympatric Lanners (Peregrines average = 1.51 young fledged per territorial pair per year, Lanners average = 2.30), although this difference was not statistically significant (Z = 1.75, P = 0.08). Pairs of either species with close neighbouring pairs of congeners were not significantly less productive than pairs with distant neighbouring pairs of congeners (Peregrines 1.17 *vs* 1.78, Wilcoxon paired-sample Z = 1.34, P = 0.18; Lanners 1.92 *vs* 2.68, Z = 1.34, P = 0.18).

Correlates of breeding success

All data pooled: Temperature and rainfall emerged as significant correlates of Peregrine breeding performance on the Cape Peninsula. Eggs were laid later with increasing rainfall (correlation coefficient r = 0.29, n = 56, P = 0.03) and rain-days (r = 0.29, n = 56, P = 0.03) in September. Clutch size, in turn, was negatively correlated with laying date (r = -0.52, n = 43, P<0.001). Breeding success correlated positively with daytime temperatures, and negatively with the amount and frequency of rainfall during the early stages of the cycle (Table 7.6). This was at least partly because severe spring weather was associated with a higher rate of egg and hatchling mortality (Fig. 7.1). Higher temperatures during the nestling period were associated with lower reproductive success by Peregrines on the Orange River, while the frequency of rainfall was positively correlated with Peregrine breeding success in the Soutpansberg (Table 7.6).

Sheltered nest ledges apparently enhanced the breeding success of Cape Peninsula and Orange River Peregrines (Table 7.6), while the height of the nest cliff and the frequency of strikes made in the vicinity of the nest correlated positively with fledging rates of

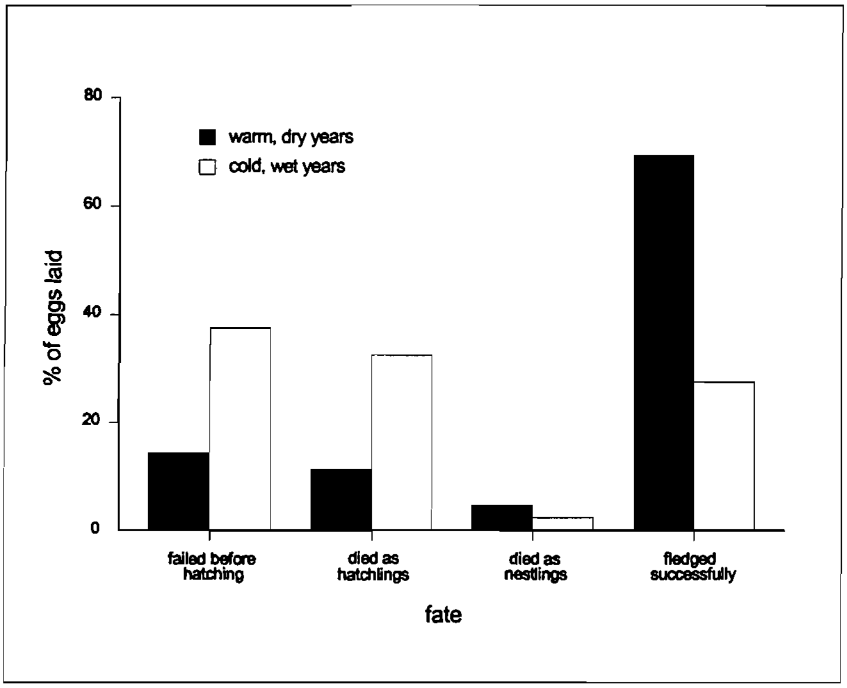


Figure 7.1 The effect of spring (September–October) weather on egg, hatchling and nestling mortality rates of Peregrines on the Cape Peninsula. Warm, dry years were 1993, 1994, and 1997, n *= 62 eggs of known fate. Cold, wet years were 1989, 1991, and 1996,* n *= 40 eggs of known fate. The two frequency distributions are significantly different (* χ^2_3 *= 19.42,* $P<0.001$*), largely because egg mortality (adjusted residual = 2.7,* $P<0.001$*) and hatchling mortality (adjusted residual = 2.6,* $P<0.001$*) were significantly higher in cold, wet years.*

Peregrines on the Cape Peninsula (Table 7.6). The floor-area of the nest ledge, the total elevation of the nest cliff and the frequency of inter- and intra-specific aggressive encounters were not correlated with the breeding performance of any of the Peregrine populations studied.

Stepwise multiple regression analysis produced a model which accounts for 45% of the variance in fledging rates per territorial pair of Peregrines on the Cape Peninsula:

> number of young fledged = 0.207 mean daily maximum temperature in September - 0.012 total exposure of nest ledge - 0.010 log rainfall in September + 0.001 height of nest cliff - 0.399, $F_{4,41} = 8.49$, $P<0.001$

Breeding success of Soutpansberg Lanners did not correlate significantly with any of the environmental variables considered in this study.

Annual productivity: Mean annual productivity of Cape Peninsula Peregrines was clearly and significantly influenced by spring weather, primarily temperature and rainfall in September (Fig. 7.2). Stepwise multiple regression analysis produced a model which accounts for 99% of the variance in average fledging success per territorial pair per year:

> number of young fledged = 0.59 mean daily maximum temperature in September + 0.04 rain-days in September - 0.08 rain-days in October - 9.54, $F_{3,5} = 162.4$, $P<0.001$

Productivity was lower on the Orange River in years with high daytime temperatures in October ($r = -0.74$, $n = 9$, $P = 0.02$) and, with the exception of one particularly unsuccessful year, was positively correlated with the height of the river during spring (Fig. 7.3). In the Soutpansberg, higher rainfall over the 12 months preceding each breeding season corresponded with higher Peregrine productivity (Fig. 7.4) but did not obviously affect Lanner breeding performance, with average fledging success only slightly depressed in 1992 (Appendix 10) – the driest year (Appendix 11).

Discussion

The timing of breeding

Egg-laying by South African Peregrines occurred progressively later with increasing latitude (Table 7.2), presumably corresponding with trends in photoperiod, climate and prey availability (Immelman 1971, Olsen 1982). However, there was no comparable cline in prey breeding activity (e.g. the peak breeding period for most columbids is from mid-October to early-November throughout the region – Harrison *et al.* 1997), so the degree of synchrony between falcon and prey breeding seasons was variable. The temperate southwest features a relatively pronounced peak in avian breeding effort (Jenkins 1991, Harrison *et al.* 1997), and egg-laying by Peregrines on the Cape Peninsula was timed to exploit increased food availability associated with this concentration of breeding prey. In contrast, Soutpansberg Peregrines bred well in advance of the (relatively diffuse) peak in prey breeding activity (Jenkins 1991, Harrison *et al.* 1997), and sympatric Lanners bred even earlier. In both species, there may be a premium on fledging young before the heat and heavy rain of summer, and before the main influx of migrant birds to the area in December–February (Harrison *et al.* 1997), which may improve foraging conditions and hence survival prospects for newly independent juveniles (e.g. Olsen & Georges 1993).

*Table 7.6 Significant correlates of Peregrine breeding performance in three areas of South Africa (1989–1997 – all data pooled). *P<0.05, **P<0.01, ***P<0.001*

breeding parameter	correlate	*r* value (*n*)
Cape Peninsula		
clutch size per breeding pair	hunts per hour of observation	0.49 (23)*
brood size per breeding pair	number of rain-days in Sept.	-0.30 (53)*
	number of rain-days in Oct.	-0.26 (53)*
young fledged per territorial pair	mean daily max. temp. in Sept.	0.49 (104)***
	mean daily max. temp. in Oct.	0.46 (105)***
	number of rain-days in Sept.	-0.41 (105)***
	total exposure of nest ledge	-0.37 (47)*
	height of nest cliff	0.34 (47)*
	hunts per hour of observation	0.37 (42)*
Orange River		
young fledged per successful pair	mean daily max. temp. in Sept.	-0.40 (28)*
	total exposure of nest ledge	-0.89 (6)*
Soutpansberg		
young fledged per breeding pair	mean daily min. temp. in Sept.	-0.38 (25)*
young fledged per territorial pair	number of rain-days in Aug.	0.31 (42)*
	number of rain-days in Oct.	0.38 (45)**

Differences in breeding performance

Although the density of Peregrine pairs on the Cape Peninsula was higher than in the other two study areas, and provisioning rates at nests and the quality of parental care observed exceeded those recorded in the Soutpansberg (Chapter 6), breeding success was relatively low (Table 7.3). Differences in data quality from each area may partly explain measured differences in fledging success, either per occupied territory or per pair attempting to breed. Occupied but inactive territories, and particularly early breeding failures, can be easily overlooked by late-season, one-visit surveys (Hickey 1969, Postupalsky 1974, Steenhof & Kochert 1982), so estimates of productivity on the Orange River and in the Soutpansberg probably were inflated in some years.

It seems unlikely that predation pressure contributed to differences in breeding performance – only one incident of nest predation was recorded, at a Peregrine site in the Soutpansberg (Jenkins 1994). Pathogenic strains of the parasitic protozoan *Trichomonas gallinae* are known from the southwestern Cape (Pepler & Oettlé 1992) and may significantly depress breeding performance in raptors (Cooper & Petty 1988), particularly species which prey on columbids, the main carriers of the disease. Hence, trichomoniasis was a possible cause of nestling mortality on the Cape Peninsula, at least in some years. Buccal cavity lesions typical of this parasite were observed in five Peregrine nestlings from three different sites on the Cape Peninsula in 1990–1991, at least two of which subsequently died. However, in a sample of seven young and five adults examined in 1994, no signs of trichomonads were detected in smears or cultures from pharyngeal swabs (Unpubl. data), and visible signs of infection were recorded in only one nestling out of 44 young and five adult Peregrines examined from 1995–1997. Lastly, although Peregrine nests on the Cape Peninsula were situated close to a major urban centre, and breeding rates may have been affected by human activities (e.g. Mearns & Newton 1988, Ratcliffe 1993), no proven incidents of persecution or illegal nest-robbing were observed or reported.

The breeding performance of Peregrines on the Cape Peninsula was highly variable between years, which effectively lowered the overall mean productivity of the population. Annual fledging rates ranged from the lowest recorded during the study (0.31 young fledged per territorial pair in 1996), to one of the highest (2.31 averaged over 16 breeding pairs in 1997) (Appendix 10). Such erratic breeding success, with large numbers of young fledged in favourable years, is typical of

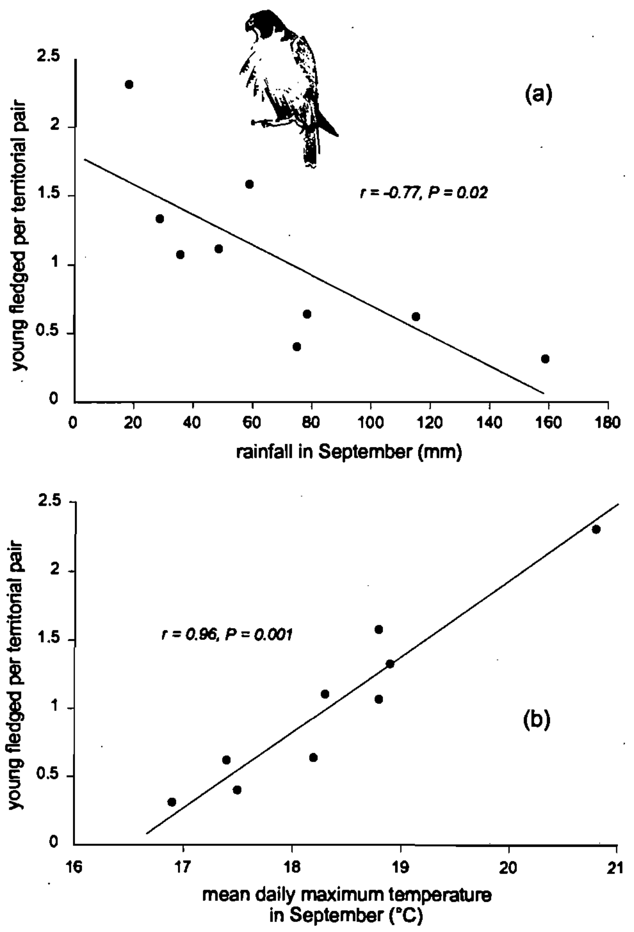


Figure 7.2 Mean annual productivity of Peregrines on the Cape Peninsula in relation to spring weather conditions. The regression equations are (a) $y = 1.79 - 0.01x$, $r^2 = 59.1\%$, $F_{1,7} = 10.11$, $P = 0.02$; *(b)* $y = 0.53x - 8.8$, $r^2 = 91.3\%$, $F_{1,7} = 73.25$, $P<0.001$.

Peregrine populations at mid- to high latitudes (e.g. Mearns & Newton 1988, Olsen & Olsen 1989b, Emison *et al.* 1993, Bradley *et al.* 1997, Norriss 1995) and reflects variability in climatic conditions (Newton 1988). Productivity on the Cape Peninsula (Table 7.3, Appendix 10) was similar to other temperate populations – e.g. south Scotland, 1.15 young fledged per territorial pair per year, range 0.60–1.45 over nine years (Mearns & Newton 1988); Canberra, southeastern Australia, 1.23 young fledged per territorial pair per year, range 0.89–1.63 over 12 years (Olsen & Olsen 1989b).

Fledging rates of Soutpansberg Peregrines and Lanners (Table 7.3) were comparable with those recorded in other published Afrotropical studies (e.g. Peregrines in Zimbabwe, 1.45 young per occupied site – Hartley *et al.* 1995, Lanners in the former Transvaal Province, 2.24 young per pair – Tarboton & Allan 1984). Although differences in reproductive output were not statistically significant, Lanners in this study generally bred more successfully than sympatric Peregrines (Table 7.3, Appendix 10), with consistently higher annual productivity, and a greater capacity to raise large broods of young. This is in accordance with suggestions in the literature (Tarboton & Allan 1984) and data from the Southern African Ornithological Society nest record card collection ('brood sizes', Lanners average = 2.67, $n = 54$, Peregrines average = 2.19, $n = 16$, $t_{68} = 1.95$, $P = 0.05$). Mean productivities of three apparently stable Peregrine populations in South Africa (Table 7.3) were equivalent to that of a declining Lanner population near Pretoria, Gauteng Province (1.3 young per pair – Kemp 1993). This could suggest fundamental differences in the population dynamics of Peregrines and Lanners in this region.

Active competition between sympatric raptor species has been demonstrated in terms of impaired reproductive output by close nesting pairs of possible competitors, relative to pairs nesting further apart (e.g. Nilsson 1984, Korpimäki 1987). While the breeding success of Soutpansberg Peregrines and Lanners with close nesting pairs of congeners was generally lower than that of more isolated pairs, these differences were not statistically significant. Hence, there was no conclusive evidence to suggest that competition between the two species affected their breeding performance.

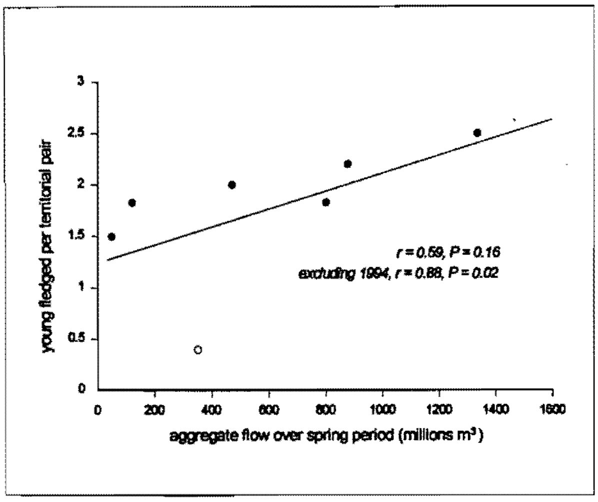


Figure 7.3 Mean annual productivity of Peregrines on the Orange River from 1989–1996 in relation to the aggregate volume of water flow in the river over the spring period (August – October). The line drawn is for the regression equation $y = 1.25 + 0.001x$, $r^2 = 34.9\%$, $F_{1,5} = 2.67$, $P = 0.16$, *calculated using the data for all years. If the outlying year 1994 (marked with an open circle) is excluded, the regression equation changes to* $y = 1.60 + 0.001x$, $r^2 = 77.9\%$, $F_{1,4} = 14.09$, $P = 0.02$.

Weather, prey availability and breeding success

Previous studies of Peregrines in temperate areas have emphasized the negative effect of spring rainfall on territory occupancy (Olsen & Olsen 1988a, Norriss 1995), breeding frequency (Olsen & Olsen 1989a) and breeding success (Mearns & Newton 1988, Olsen & Olsen 1989b, Emison *et al.* 1993). In particular, frequent, heavy rain immediately before, during and after incubation may flood exposed nest ledges and prevent or delay egg-laying (Olsen & Olsen 1989a), cause the abandonment or chilling of clutches, soak and kill hatchlings (Olsen & Olsen 1989b, Emison *et al.* 1993) and reduce the foraging efficiency of provisioning males (Mearns & Newton 1988). Temperature was generally a secondary correlate of breeding performance by these populations, with cold conditions exaggerating the negative effects of rainfall.

On the Cape Peninsula, mean daily maximum temperature over the laying and incubation period strongly and positively affected fledging success (Table 7.6, Fig. 7.2), while spring rainfall reduced egg hatchability and hatchling survival (Table 7.5, Figs 7.1 & 7.3, also see Chapter 2 for information on the effect of rainfall on nest site selection). The absence of a significant, negative relationship between breeding success and minimum temperatures suggests that warmer conditions did more than simply mitigate the negative effects of rainfall. Breeding activity of *Streptopelia* doves (staple prey of Peregrines on the Cape Peninsula – Chapter 5) in the southwestern Cape generally peaks in October/November (Harrison *et al.* 1997). Rowan (1983), using nest record data for Cape Turtle doves *S. capicola*, found that heavy, late-winter rain tends to delay this peak, while dry weather in July and August advances it. Re-analysis of Rowan's data to assess the influence of spring temperatures on the breeding seasons of doves suggests an association between warm Septembers and early breeding, with the warmest September in the dataset (1960, mean daily maximum 20.6°C) corresponding with the earliest, most clearly defined peak in dove breeding activity. Therefore, spring weather on the Cape Peninsula may affect Peregrine productivity mainly by regulating columbid breeding patterns, and hence the availability of inexperienced fledgling doves as prey early in the falcon breeding cycle. As evidence for this, the proportion of juvenile columbids in the diet of Cape Peninsula Peregrines each year from 1989–1995 (see Chapter 5 for methodology) ranged from 0–16%, and was positively correlated with daytime temperatures in September (Spearman's rank correlation coefficient $r_s = 0.84$, $n = 7$, $P = 0.04$).

Positive relationships between Peregrine breeding success and flow rates on the Orange River (Fig. 7.3) or the previous season's rainfall in the Soutpansberg (Fig. 7.4), suggest a similar emphasis on local prey availability. Both these parameters are possible indices of primary productivity and bird abundance. Higher water levels on the Orange River increase habitat availability for water-borne dipteran larvae and raise the rate of emergence of adult flies (Palmer 1997). Burgeoning insect populations are likely to attract large numbers of aerial insectivores (swifts, hirundines and microchiropteran bats) to the floodplain, increasing prey availability for provisioning falcons.

Avian productivity in the woodland adjacent to the Soutpansberg range is probably higher in wet years (e.g. Tarboton 1980), which arguably increases the absolute abundance of birds available as prey in the next spring. Also, rainfall may have a lagged effect on productivity in African savannas, with the previous season's rain influencing the fruit yield and the timing of leaf

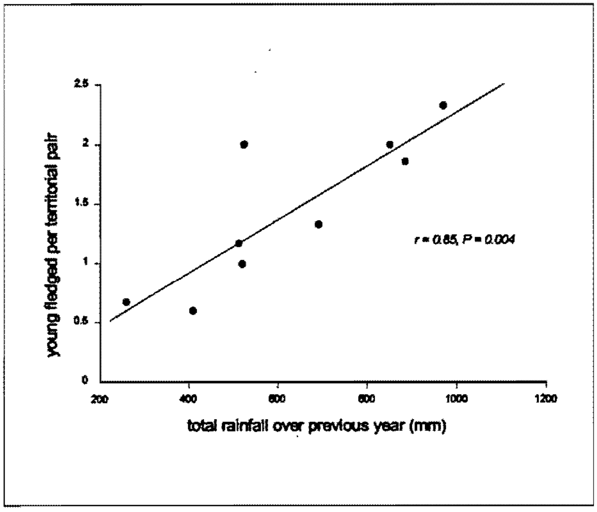
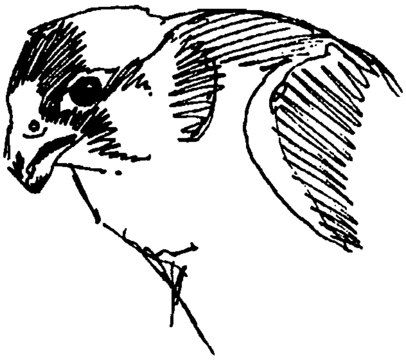


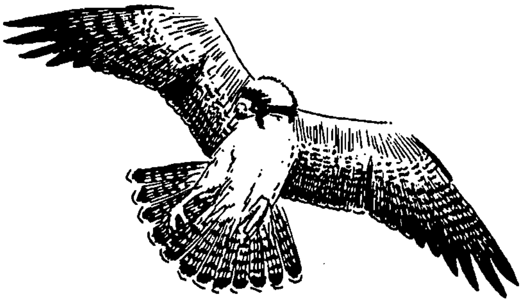
Figure 7.4 Mean annual productivity of Peregrines in the Soutpansberg in relation to rainfall over the previous 12 months. The regression equation is $y = -0.045 + 0.002x$, $r^2 = 71.6\%$, $F_{1,7} = 17.67$, $P = 0.004$.

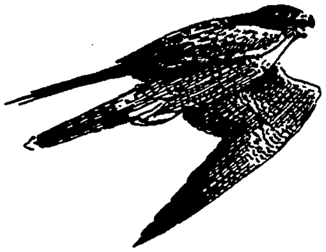
emergence and associated increases in arthropod abundance (Vernon 1978, Earlé 1982). This may determine the timing of breeding by woodland birds and probably also affects overall avian abundance early in the season, which in turn affects Peregrine breeding success. Kemp (1991) found a similar relationship between the breeding performance of Greater Kestrels *F. rupicoloides* on a grassland-savanna ecotone, prey availability and rainfall in the preceding year.

Falcons in each area typically used nest sites which met certain minimum, physical criteria (Chapter 2), but not all these criteria affected the outcome of a breeding attempt once it commenced. Nest ledge size and the elevation of the nest site were distinguishing features of the microhabitat requirements of falcon populations in this study (Chapter 2) but did not influence reproductive success. However, sheltered nest ledges improved breeding success on the Cape Peninsula and the Orange River, presumably because they reduced the incidence of failures attributable to heavy rain or heat extremes respectively. In addition, higher cliffs were advantageous to Peregrine pairs on the Cape Peninsula (Table 7.6), perhaps because they afforded more protection from terrestrial predators (Mearns & Newton 1988), but probably because they provided better foraging opportunities for provisioning adults (Chapters 2 & 4).

Generally, Peregrine breeding success reflected fluctuations in the physical environment, but probably was largely regulated by the effects of these fluctuations on prey availability (e.g. Village 1986, Kostrzewa & Kostrzewa 1990, Steenhof *et al.* 1997).







Chapter Eight

Factors limiting Peregrine populations in tropical environments: interspecific competition or resource deficiency?

"The strength of circumstantial evidence is a function of the care with which a study is conducted, ..." (John A. Wiens, The ecology of bird communities, Vol. 2, *Cambridge University Press 1989)*

***Summary** – Density and productivity of Peregrine populations correlate positively with latitude, while habitat selectivity increases with proximity to the Equator. Where Peregrines are rare in the tropics they may be outcompeted by similar congeners (e.g. the Lanner), which replace them in many areas. Alternatively, tropical Peregrines may be limited by resource deficiencies which do not affect their close relatives. Data from Peregrine and Lanner populations in South Africa support the resource limitation hypothesis, and there is no evidence to suggest proximate competition between the two species. Morphological and behavioural specialization probably restricts Peregrines to optimal foraging conditions in areas where prey are not spatially or temporally concentrated, or otherwise particularly vulnerable to attack. The relative dynamics of Arctic and temperate vs tropical prey populations is suggested as an important factor determining Peregrine distribution globally. Populations of other widespread but particularly specialized avian predators (e.g. Osprey) may be similarly controlled. Food limitation in the tropics has resulted in specialization and rarity in Peregrines and generalization and relative abundance in desert falcons.*

Introduction

Although the Peregrine occupies an extensive aggregate range over a wide variety of environmental conditions (Cade 1982, del Hoyo *et al.* 1994), it is relatively unsuccessful in the tropics. Peregrines are patchily distributed and uncommon in sub-Saharan Africa (Cade 1969, Brown *et al.* 1982, Mendelsohn 1988, although see Thomsett 1988, Pepler *et al.* 1991, Hartley 1992), southern Asia (Cade 1982), northern Australia (Olsen & Olsen 1988b) and southern North America (Hunt *et al.* 1988, Porter *et al.* 1988), and they are completely absent from northern and eastern South America (McNutt *et al.* 1988). This pervading rarity may be attributed to competition with similar congeners (e.g. Lanners – Tarboton & Allan 1984, Thomson 1984, Mendelsohn 1988, and Prairie Falcons *F. mexicanus* – Porter & White 1973), or it may be symptomatic of generally low resource availability in tropical environments (Mendelsohn 1988, Jenkins 1991).

This chapter reviews recent Peregrine population studies to further substantiate postulated latitudinal trends in nest site use, density and breeding performance (Jenkins 1991). Data from previous chapters are synthesized in an overall assessment of factors limiting South African Peregrine populations, with emphasis on the relative importance of competition with sympatric Lanners *vs* more direct, environmental constraints. This evaluation is then set in the wider context of other

Table 8.1 Mean breeding performance of Peregrines across a range of latitudinal zones, based on data from recent studies of pristine or recovered populations (see Appendix 12)

zone	*n* studies	*n* pair-years	young fledged per territorial pair	young fledged per successful pair
high Arctic (65° N +)	6	849	1.81	2.54
subarctic (55–64° N)	7	1494	1.57	2.40
temperate (30–54° N/S)	19	2891	1.51	2.17
subtropical (25–29° N/S)	3	196	1.34	2.17
tropical (<25° N/S)	3	90	1.42	1.92

sympatric populations of Peregrines and congeners, relating predatory specialization to latitude and the dynamics of prey populations.

Methods

Nest site selection, density and breeding performance data were extracted from recent (post–1980), published studies of Peregrine populations. Many contemporary studies focus on the productivity of falcon populations affected by the use of organophosphate pesticides, or on the dynamics of recolonisation in areas where the species was previously extinct. As far as possible, such studies were not included in this analysis, and only data from naturally regulated populations – i.e. those believed to be relatively free from anthropogenic influences – were used . Some of the source publications (especially those in Cade *et al.* 1988) document the breeding history of Peregrine populations both during and after decreases associated with chemical contamination. In such cases, only data from the latter period were used. Sample sizes for each study were expressed in terms of pair-years, and studies conducted over multiple breeding seasons were preferred to single-season surveys. However, in the interests of the geographic scope of the analysis, some studies of small populations over short time periods were included, mostly from tropical and subtropical areas.

Correlation analysis was used to test the statistical significance of latitudinal trends in nest site selection, density and productivity. These trends were examined within the Northern and Southern Hemispheres, and within the New and Old Worlds, as well as globally.

Methods used in studying the biology of Peregrines and Lanners in South Africa are presented in Chapters 1–7.

Results & discussion

Latitude and the performance of Peregrine populations

Thirty-eight studies contributed data to this analysis (Appendix 12). Most of these were from northern and temperate regions, and few data were available for tropical and subtropical populations (Table 8.1, Appendix 12). Relatively few studies included usable data on nesting habitat use, the density of breeding pairs and clutch size. Most were extensive, late-season population surveys, with limited information on territory occupancy and the actual number of pairs attempting to breed (Postupalsky 1974, Chapter 7). Hence, the number of young fledged per successful pair was considered the most reliable criterion for comparing breeding performance, although it probably provided inflated estimates of productivity (Steenhof & Kochert 1982).

Globally, nesting habitat selectivity (in terms of the critical variable, nest cliff height – Chapter 2) was negatively correlated with latitude (Table 8.2, Fig. 8.1). Although habitat availability in each area generally was not documented, the lower minimum height of cliffs used by temperate and Arctic populations (Table 8.2, Fig. 8.1) is particularly suggestive of a greater tolerance of suboptimal nesting conditions (e.g. widespread ground-nesting is restricted to high Arctic areas – Cade 1982, Lindberg *et al.* 1988).

Across the entire sample of studies, clutch size and young fledged per successful pair were positively correlated with latitude (Tables 8.1 & 8.2, Fig. 8.2). These trends were generally present within each hemisphere and in the New and Old World subsamples, where sufficient studies were available for inclusion (Table 8.2). Inter-pair distance, as a measure of breeding density, was not significantly correlated with latitude

***Table 8.2** Mean nest site use, density and breeding performance of Peregrine populations around the world (see Appendix 12) in relation to latitude. Data provided are correlation coefficients with sample sizes in parentheses (n.s. = not significant, *P<0.05, **P<0.01, ***P<0.001)*

variable	northern hemisphere	southern hemisphere	Old World	New World	global
mean cliff height	-	-0.83 (7) *	-	-	-0.86 (9) **
minimum cliff height	-	-0.95 (8) ***	-	-	-0.68 (11) *
inter-pair distance	-0.77 (7) *	0.17 (6) n.s.	-0.54 (9) n.s.	-	-0.40 (13) n.s.
clutch size	0.27 (7) n.s.	-	0.69 (8) n.s.	-	0.75 (10) *
young fledged per territorial pair	0.40 (25) *	0.20 (11) n.s.	-0.22 (17) n.s.	0.48 (15) n.s.	0.22 (36) n.s.
young fledged per successful pair	0.67 (26) ***	0.60 (11) *	0.05 (16) n.s.	0.77 (17) ***	0.57 (37) ***

globally. However, there was a significant negative relationship between latitude and density in the northern hemisphere, where the most comprehensive studies of the largest sustained populations have been made (Appendix 12).

Overall, the largest, densest and most productive Peregrine populations occur at high latitudes (e.g. north and central Greenland – Mattox & Seegar 1988, and the Canadian Arctic – Court *et al.* 1988, Bradley *et al.* 1997), while the sparsest, least productive populations, and those most obviously limited (at least proximately) by the availability of suitable nesting habitat, occur in the tropics (e.g. Peru and Ecuador – McNutt *et al.* 1988, and northeastern South Africa – Tarboton & Allan 1984). Note that this does not necessarily imply a difference in the fitness of Peregrines in temperate *versus* tropical environments. While the tropics may constitute inherently low quality Peregrine habitat, this disadvantage may be offset by a reduction in negative, density-dependent effects on lifetime reproductive success (Fretwell & Lucas 1969). For example, tropical Peregrines living at low densities may be subject to lower levels of intraspecific competition, and may be longer lived as a result.

Over most of North America, Eurasia and Africa, Peregrines are sympatric with the 'desert falcon' complex of similar species (subgenus *Hierofalco,* comprising the Lanner, Lagger Falcon *F. jugger,* Prairie Falcon, Saker Falcon *F. cherrug* and Gyrfalcon *F. rusticolus* – Cade 1982). Desert falcons tend to be more prolific in subtemperate and tropical regions (Table 8.3). Between 30° N and 30° S, Lanners, Laggers and Prairie Falcons are the most common large falcons within their respective ranges (Ali & Ripley 1978, Brown *et al.* 1982, Cade 1982). Hence, there is reason to suspect competitive interactions between Peregrines and congeners which benefit the latter in tropical environments, especially given that hierofalcons generally breed earlier in the season than sympatric Peregrines (Ali & Ripley 1978, Porter & White 1973, Chapter 7) and conceivably prevent them from using otherwise suitable nest sites (Porter & White 1973, Thomson 1984, Mendelsohn 1988).

Evidence from South Africa

Latitudinal trends in nesting habitat use, density and productivity of Peregrines within South Africa generally comply with global patterns. Certainly, Peregrines are most common and widespread in the temperate southwest, and rare, patchy and restricted to high cliffs in the tropical northeast (Tarboton & Allan 1984, Chapters 1 & 2). Lanners exhibit roughly the opposite trend (Chapter 1). Without experimental evidence, these contrasting distribution patterns cannot be conclusively

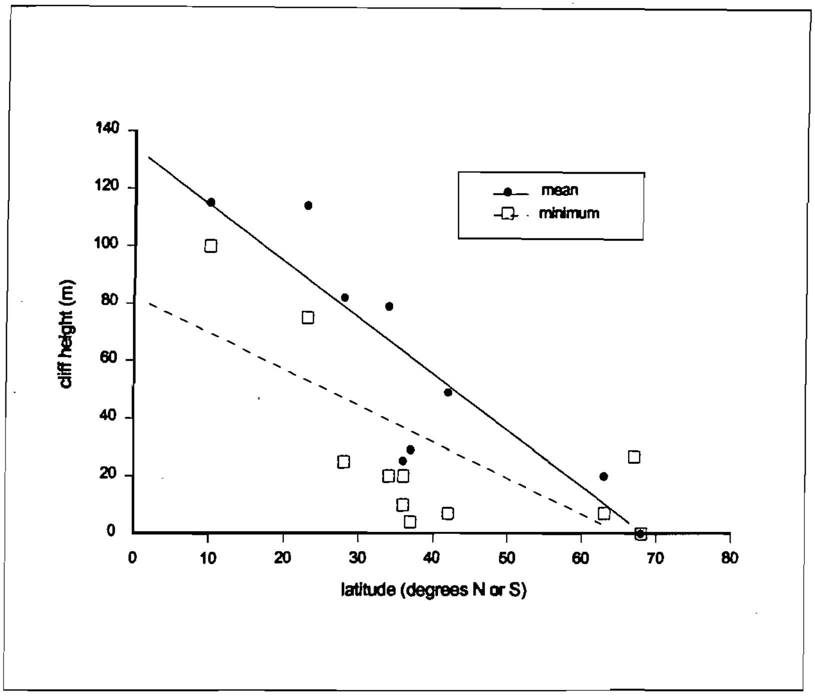


Figure 8.1 Peregrine nesting habitat selectivity, measured in terms of mean and minimum nest cliff height, in relation to latitude. Data are from recent studies of pristine or recovered populations. See Table 8.2 for correlation coefficients.

ascribed to either interspecific competition or resource limitation (Newton 1980, Connor & Simberloff 1986, Wiens 1989). However, sufficient observational data have been accumulated from sympatric populations to examine the relative strength of these hypotheses in light of theoretical predictions.

Interspecific competition: Phylogenetic relatedness, similarities in ecomorphology, significant niche overlap, correlated changes in niche dimensions with changing environmental conditions and high frequencies of interspecific aggression are all features of sympatric populations considered to enhance the likelihood of interspecific competition, or to be circumstantial evidence of its effects (Wiens 1989). Morphologically, Peregrines and Lanners are very similar (Chapter 3). Comparisons of size and key food handling and flight performance measurements (Table 8.4) yield ratios consistently lower than values traditionally considered minimum for non-competitive coexistence (1.3 for linear measurements, 2.1 for non-linear measurements – Hutchinson 1959, although see Simberloff & Boecklen 1981, Schoener 1984).

Despite these structural similarities, diet overlap of sympatric Peregrines and Lanners in the Soutpansberg was fairly low (Morisita's $C = 0.34$ – Chapter 5), and the presence of close neighbouring pairs of congeners did not significantly affect dietary niche width (Chapter 5). Hence, there was no evidence of direct competition

***Table 8.3** The relative status of Peregrines and sympatric desert falcons at different latitudes*

latitude	Peregrine race	relative status	desert falcon
Arctic	*tundrius*	common / uncommon[a]	Gyrfalcon
	peregrinus	common / rare[b]	Lanner
temperate	*anatum*	uncommon / common[c]	Prairie
	cassini	common / absent[d]	
	macropus	common / absent[e]	
	minor	rare / common[f]	Lanner
tropical	*peregrinator*	rare / common[g]	Lagger

References: [a]Cade 1960, Court *et al.* 1988, Poole & Bromley 1988; [b]Cade *et al.* 1988, Massa *et al.* 1991, Manzi & Perna 1994; [c]Porter & White 1973, Cade *et al.* 1988; [d]McNutt *et al.* 1988; [e]Olsen & Olsen 1988b, 1989; [f]Brown *et al.* 1982, Steyn 1982, Chapter 1; [g]Ali & Ripley 1978, Cade 1982

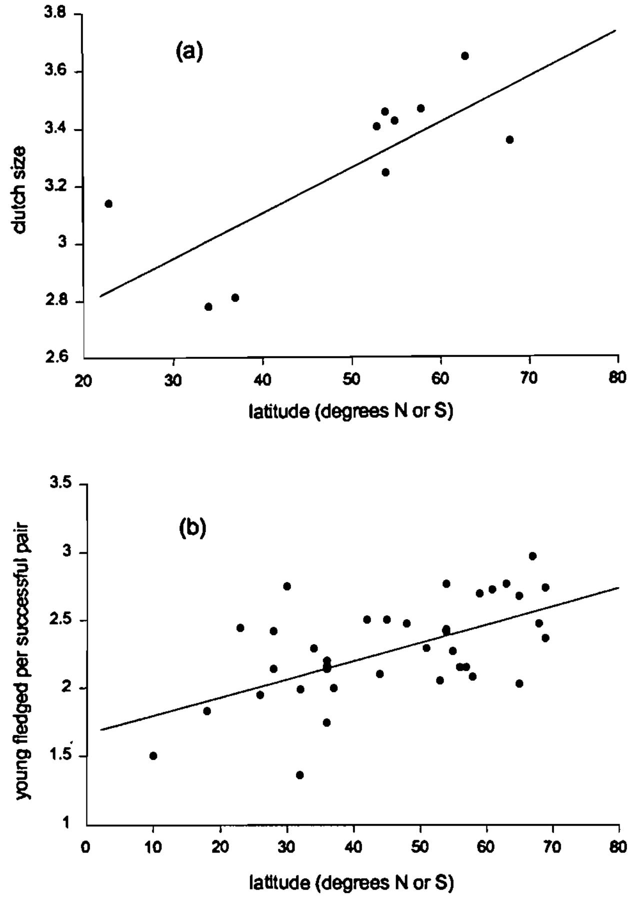


Figure 8.2 Peregrine breeding performance, measured in terms of (a) mean clutch size and (b) the average number of young fledged per successful pair, in relation to latitude. Data are from recent studies of pristine or recovered populations. See Table 8.2 for correlation coefficients.

for food. However, although foraging habitat preferences of the two species (inferred from the habitat affinities of identified prey) were significantly different (Chapter 5), they overlapped considerably (C = 0.63, calculated using the raw data contributing to option *B* in Table 5.8). This implies overlap in foraging ranges, and raises the possibility of interference competition between Peregrines and Lanners hunting in the same areas. This was particularly likely given that daily provisioning schedules of breeding pairs of the two species were not significantly different (Chapter 6), so foraging may have coincided temporally as well as spatially.

Superficially, there was extensive overlap in nesting habitat use by the two falcon species in the Soutpansberg (Chapter 2). However, typical nest sites were significantly different in 10 out of 32 measured variables, and over 90% were correctly identified to species by discriminant function analysis (Chapter 2). The output of this analysis was used to measure overlap in nesting habitat requirements (see Bosakowski *et al.* 1992), yielding a value of only 0.32. Thus, even on the fairly homogeneous Soutpansberg cliff-line, microhabitat requirements of nesting Peregrine and Lanner pairs were distinct.

Territorial aggression between species is considered particularly good evidence of competition (Wiens 1989). During this study, interactions between Peregrines and Lanners comprised only 40 (5.3%) of 758 aggressive incidents recorded in falcon territories, and aggression between congeners was generally less frequent than intraspecific aggression (Table 8.5). In conditions of direct sympatry (Soutpansberg, Augrabies Falls National Park), skirmishes between Peregrines and Lanners made up only 13 (5.4%) of 239 aggressive incidents. Of these, only eight involved intruding adults, and only one was recognized as conflict for territory between established pairs. No instances of territory usurpation or replacement of Peregrines by Lanners or *vice versa* were observed (but see Thomson 1982, Thomsett 1988), and in all aggressive encounters between these two species territory holders repelled intruders, with neither species consistently dominant. In the Soutpansberg, close neighbouring pairs of congeners did not significantly impair the breeding performance of Peregrine or Lanner pairs (Chapter 7). This is further testimony to an absence of interference competition between the two species (cf. Korpimäki

Table 8.4 Ratios (largest to smallest) comparing body mass and measurements of key food handling and flight performance features of southern African Peregrines and Lanners (calculated from means in Appendix 5)

	males	females
body mass	1.04	1.05
bill length	1.01	1.02
wing span	1.10	1.09
wing length	1.11	1.10
secondary length	1.21	1.19
inner rectrix length	1.20	1.24
tarsus length	1.06	1.02
toe 2 length	1.07	1.13
toe 4 length	1.14	1.17
wing loading	1.36	1.30
aspect ratio	1.07	1.04

1987, Kostrzewa 1991).

The accumulated evidence (Table 8.6) does not support the contention that African Peregrine populations are limited by proximate competition with sympatric Lanners. Mean niche overlap (Holt 1987, Bosakowski *et al.* 1992) between sympatric populations in the Soutpansberg was about 0.4, well below the theoretical 'competition threshold' value of 0.6 (Bosakowski & Smith 1992, Bosakowski *et al.* 1992). However, the possibility that existing distributions, behaviours and resource partitioning are the result of past competitive interactions between the two species cannot be discounted (Wiens 1989).

Resource limitation: Food and nest sites are the resources which most commonly limit raptor populations (Newton 1979), although physiological constraints (e.g. heat tolerance and dependence on free water) may contribute, and have been suggested as factors affecting the distribution of Peregrines in Africa (Mendelsohn 1988). Reduced tolerance of suboptimal nesting habitats (Chapter 2) effectively reduces nest site availability for tropical and subtropical Peregrine populations in South Africa. However, given that nesting habitat quality affects the foraging efficiency of resident pairs (Chapter 4), nest site selectivity may be expected to correlate negatively with food abundance or availabilty. In this way, populations proximately limited by nest site availability may ultimately be limited by food and its defining effect on the utility of breeding areas (Jenkins 1991).

General correlations between falcon productivity and indices of environmental productivity emphasize the importance of food in limiting Peregrine populations in South Africa (Chapter 7) and other areas (e.g. Ratcliffe 1993, Thiollay 1988). Circumstantial evidence of relative food shortage at tropical (Soutpansberg) nests in relation to temperate (Cape Peninsula) nests included lower provisioning rates, inferior parental care and greater foraging effort by Soutpansberg pairs (Chapter 6, Newton 1978). Nestling growth rates seemed slightly retarded in the Soutpansberg (Chapter 6), although no physical signs of food deprivation were observed in either area, and rates of egg and hatchling mortality were higher on the Cape Peninsula (Chapter 7).

Productivity of the two populations was not significantly different, and was subject to considerable

Table 8.5 Incidence of inter- and intraspecific aggression recorded at Peregrine and Lanner nest sites in South Africa, with emphasis on the relative frequency of aggression between Peregrines and intruding Lanners and vice versa

population	frequency[a] of interspecific aggression[b]	frequency[a] of intraspecific aggression	aggression between congeners		
			frequency[a] (*n*)	% adults intruding	% pairs intruding
Peregrines					
Cape Peninsula	0.11	0.04	0.01 (25)	4	0
Orange River	0.10	0.02	0.01 (6)	17	0
Soutpansberg	0.26	0.01	0.01 (4)	75	0
Lanners					
Orange River	0.20	0.02	0.04 (4)	100	25
Soutpansberg	0.20	0.03	0.01 (1)	0	0

[a] mean number of incidents per hour of observation
[b] involving species other than Lanners/Peregrines

***Table 8.6** Factors limiting Peregrines in tropical environments: South African evidence for and against (a) competition with congeners and (b) resource deficiency*

evidence for	evidence against
(a) proximate competition with sympatric Lanners	
1. opposite trends in distribution	1. low diet overlap
2. similar ecomorphology	2. diet unaffected by close neighbouring congeners
3. moderate overlap in foraging habitats and times	3. low nesting habitat overlap
	4. breeding unaffected by close neighbouring congeners
	5. little aggression between congeners
(b) resource deficiency in the Soutpansberg (*vs* the Cape Peninsula)	
1. more stringent nesting habitat requirements	1. lower egg and hatchling mortality
2. lower density of breeding pairs	2. higher mean annual productivity
3. lower hunting rates in the vicinity of nest sites	
4. lower provisioning rates at nests	
5. less parental attendance at nests	
6. greater foraging effort by breeding pairs	
7. inferior nestling growth rates	
8. lower frequency of large broods of young	

inter-annual fluctuation, especially on the Cape Peninsula (Chapter 7). Given that the difference in the latitudes of the Cape Peninsula and Soutpansberg study areas was relatively small (11°), and that the temperate population was non-migratory (and therefore was unlikely to exhibit the more extreme effects of latitude on life history traits typical of northern populations - see Greenberg 1980), conspicuous differences in productivity may not have been a realistic expectation. Also, the relative influence of variability in individual breeding performance on these small samples could not be accounted for, but may have been significant (e.g. Newton 1986, Mearns & Newton 1988). Nevertheless, although the frequency of small broods of young was higher on the Cape Peninsula than in the Soutpansberg (Chapter 7), more large broods were fledged on the Cape Peninsula, suggesting that the reproductive *potential* of this population was greater.

Evidence from other sympatric populations: Relations between sympatric Peregrine and desert falcon populations have also been examined in Arctic (e.g. Cade 1960, Poole & Bromley 1988) and northern temperate environments (e.g. Porter & White 1973, Massa *et al.* 1991, Manzi & Perna 1994). These studies generally found effective dietary segregation (see Table 5.9) between falcon populations. However, in two cases at least, the species with the most specialized nest site requirements (Alaskan Gyrfalcons and Peregrines in northern Italy) were considered to restrict the range of their less selective counterparts (Peregrines and Lanners respectively) by limiting access to otherwise usable habitat (Cade 1960, Manzi & Perna 1994). This interpretation suggests that African Peregrines may competitively exclude Lanners from certain areas, rather than the reverse.

Overall, the results of this study support the resource deficiency hypothesis, with food limitation presenting the most convincing explanation for the rarity of Peregrines in tropical environments (Table 8.6).

Latitude, avian productivity and prey availability

Bird-eating hawks generally achieve low hunting success rates and low energy returns per unit foraging time (Temeles 1985). Success in strikes at flying birds is strongly influenced by qualities of the predator, its prospective prey and the structure of the underlying habitat (e.g. Kenward 1978, Chapter 4). Such sensitivity accentuates the distinction between the abundance of prey in a given environment, and prey availability in terms of its vulnerability to attack (Temeles 1985). This discrepancy may be further exaggerated in the feeding ecology of large falcons, which typically hunt birds at high speeds in open, three-dimensional airspace (Cade 1982, Chapters 3 & 4).

While Peregrines often have a greater diet breadth than sympatric congeners (Chapter 5), the latter consistently take a higher proportion of non-avian or terrestrial prey (e.g. Cade 1960, Porter & White 1973, Massa *et al.* 1991, Chapter 5). This may be explained in terms of subtle differences in flight morphology and energetics, which promote a relatively sedentary hunting mode in Peregrines (and a tendency to take active, aerial prey) and more active foraging by desert falcons (and a greater capacity to take sedentary prey on the ground – Chapter 3). As more specialized bird predators, it follows that Peregrine distribution should be more directly influenced by the dynamics of bird populations, and more sensitive to the effects of habitat structure (particularly nest cliff height) on the vulnerability of aerial prey.

In light of this perceived sensitivity, Peregrine prey availability may be fundamentally tied to latitudinal trends in avian breeding strategies (Jenkins 1991). Bird breeding seasons are more synchronous and more productive with increasing latitude (Ricklefs 1980, Wyndham 1986). This concentration of the breeding effort is likely to provide flushes of displaying, provisioning and newly-fledged birds, particularly vulnerable to predation by Peregrines (Chapter 4). Exploitation of such an abundant source of available prey may be what permits Peregrines in Arctic environments to obtain higher sustained densities and achieve greater breeding success than populations elsewhere (Table 8.1, Fig. 8.1), even without the benefit of high cliffs to facilitate foraging (Fig. 8.2, Chapter 4). Conversely, increasingly aseasonal and less productive avian breeding towards the tropics (Ricklefs 1980, Wyndham 1986), may lower the overall quality of the Peregrine prey base, restricting breeding pairs to optimal habitats (high cliffs) which are limiting in the environment.

This hypothesis predicts that prey breeding regimes are particularly influential in the timing and success of Peregrine breeding cycles at high latitudes. Recent studies of Arctic Peregrines suggest that this is the case. Falcon breeding apparently is timed to coincide with the fledging period of local passerine populations (Falk *et al.* 1986, Court *et al.* 1988), and fledgling or juvenile birds comprise 'the bulk' (perhaps 60–70%) of prey delivered to active nests in some areas (Court *et al.* 1988, Rosenfield *et al.* 1995).

The 'prey productivity' theory is largely supported (but not tested) by data from South Africa. Avian breeding seasons are generally shorter, more synchronized and more productive in the temperate southwestern parts of the country than in the subtropical/tropical northeast (Winterbottom 1963, Jenkins 1991, Harrison *et al.* 1997). Correspondingly, Peregrines preyed on juvenile birds more frequently on the Cape Peninsula than in the Soutpansberg (Chapter 5), and the proportion of juveniles taken by breeding pairs on the Cape Peninsula was sensitive to correlates of prey breeding seasonality and success, as was the overall productivity of the population (Chapter 7).

While other studies have noted that tropical populations of widespread raptor taxa appear to be limited by food (e.g. Simmons 1986, Beissinger 1990), this hypothesis is unique in linking density to prey availability via a changeable definition of habitat quality. Ultimately, Peregrines are limited by specialized morphology and behavioural stereotypy which restricts foraging mode, and places increasing emphasis on habitat quality as food conditions decline. Few avian predators are as widespread and specialized in their manner of securing prey as the Peregrine. Consequently, few species are likely to exhibit the same degree of responsiveness to global patterns of productivity. However, parallels in Peregrine and Osprey *Pandion haliaetus* biology suggest that the ideas presented here may be more widely applicable. The Osprey has a cosmopolitan distribution and feeds entirely on fish, caught in spectacular, vertical dives (del Hoyo *et al.* 1994). Foraging efficiency is profoundly influenced by the physical structure of water bodies and the abundance and dispersion of prey (Swenson 1979, Poole 1989), and clutch sizes and provisioning rates at nests are positively correlated with latitude (Poole 1982, 1989).

Jack-of-all-trades or master of one? Specialization and the distribution of large falcons

Functionally, Peregrines and desert falcons represent variations on a common theme, and are similarly designed as fast-flying predators of birds. These qualities are emphasized in the Peregrine group (and particularly in tropical Peregrines, Taita Falcons and Orangebreasted Falcons) to the extent that its success in any environment is largely dependent on the concentration or vulnerability of the avian prey base, and the effects of topography on foraging conditions (Beebe 1974). The desert falcons have retained a degree of plasticity in foraging mode and nesting habitat requirements. The two groups show opposing responses to postulated latitudinal trends in prey availability: niche contraction and rarity (Peregrines) *vs* niche expansion and relative abundance (hierofalcons) with decreasing resource availability towards the Equator.

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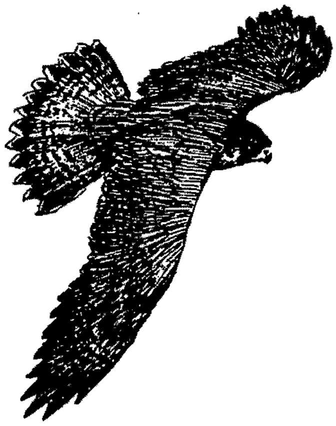

Appendices

***Appendix 1** Reporting rates of Peregrines and Lanners in the breeding and non-breeding seasons, in relation to the distribution of vegetation types and BIOMES in South Africa*

cliff category	breeding		non-breeding		
	NR[a]	RR%[b]	NR	RR%	χ^2;sig.[c]
Peregrines					
Succulent Karoo	8	0.61	5	0.34	1.05
Nama Karoo	14	0.70	17	0.58	0.27
Grassy Karoo	3	0.27	1	0.07	1.49
KAROO	25	0.57	23	0.40	1.47
Central Kalahari	7	0.57	3	0.15	4.31
Southern Kalahari	2	0.52	6	0.75	0.20
KALAHARI	9	0.56	9	0.32	1.40
Arid Woodland	11	0.99	7	0.41	3.62
Mesic Woodland	33	0.53	23	0.26	7.15
Mopane Woodland	2	0.29	4	0.45	0.25
WOODLAND	46	0.58	34	0.30	8.79
Sweet Grassland	0	0	1	0.04	0.73
Mixed Grassland	18	0.45	18	0.32	1.07
Sour Grassland	15	0.13	34	0.22	2.71
GRASSLAND	33	0.19	53	0.23	0.48
FYNBOS	81	1.01	148	1.44	6.66
Lanners					
Succulent Karoo	49	3.63	91	6.42	10.59
Nama Karoo	126	5.86	272	9.87	23.96*
Grassy Karoo	42	3.68	92	6.42	9.15
KAROO	217	4.68	455	8.11	45.79***
Central Kalahari	12	0.91	65	3.47	21.05*
Southern Kalahari	77	17.99	262	34.56	26.29**
KALAHARI	89	5.09	327	12.42	59.49***
Arid Woodland	30	2.60	72	4.29	5.35
Mesic Woodland	269	4.20	301	3.50	4.89
Mopane Woodland	10	1.46	33	3.77	7.47
WOODLAND	309	3.75	406	3.63	0.17
Sweet Grassland	63	3.66	127	5.30	5.84
Mixed Grassland	153	3.84	272	4.72	4.20
Sour Grassland	696	6.17	902	5.90	0.66
GRASSLAND	912	5.37	1301	5.56	0.68
FYNBOS	156	1.93	480	4.71	100.57***

[a]Number of SABAP records; [b]Reporting rate; [c]χ^2_1 value and level of significance of difference between reporting rates in the breeding and the non-breeding season (*$P<0.05$, **$P<0.005$, ***$P<0.001$)

Appendix 2 Abbreviations, definitions, technniques and units used to measure the variables describing falcon nesting habitats

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Nest ledge parameters
(centred on the scrape where the eggs were laid)

HTRF	Vertical height of the roof (tape measure; cm)
LTFL	Horizontal length of the floor (tape measure; cm)
WTOV	Horizontal width of the overhang above the site (tape measure; cm)
WTFL	Horizontal width of the floor (tape measure; cm)
VEXP	Vertical exposure: the angle from the scrape to the outer edge of the two sides (protractor; degrees)
HEXP	Horizontal exposure: the angle from the scrape to the outer edge of the roof (protractor; degrees)
TEXP	Total exposure (VEXP + HEXP; degrees)
AENT	Area of the entrance (HTRF x LTFL; m^2)
AFLO	Area of the floor (LTFL x WTFL; m^2)
ASST	Directional aspect relative to true north: (1) 136–180° (2) 91–135° (3) 46–90° (4) 1–45° (5) 181–225° (6) 316–0° (7) 226–270° (8) 271–315° (read from 1:50 000 topographical maps; sectors 1–8 in order of increasing exposure to hot, afternoon sun)
TPST	Type of site: (1) pothole (2) covered ledge (3) horizontal crack (4) vertical crevice (5) open ledge (categories 1–5 in order of increasing exposure)
HTSP	Relative height of the nest ledge on the cliff (climbing rope of known length used to measure height of the site above ground/HTCL x 100; %)

Nest cliff parameters
(centred on the nest ledge)

AASL	Altitude above sea level (1:50 000 topographical maps; m)
HTCL	Vertical height (measured using a climbing rope of known length; m)
LTCL	Horizontal length (1:50 000 topographical maps; m)
VERC	Verticality: (1) overhung (2) >vertical (3) vertical (4) <vertical (5) sloped (categories 1–5 in probable order of decreasing protection against weather and terrestrial predators)
ACL	Area of the nest cliff (HTCL x LTCL; m^2)
ASCL	Directional aspect of the nest cliff (categories 1–8 as for ASST)
TPCL	Type of cliff: (1) isolated cliff (2) range promontory (3) range outlier (4) escarpment (5) cliff with hills (6) gorge (categories 1–6 in order of decreasing prominence)
STFC	Structure of the cliff face: (1) potholes, horizontal and vertical cracks (2) horizontal and vertical cracks (3) horizontal cracks (4) vertical cracks (5) mostly smooth (categories 1–5 in order of decreasing availability of potential nest ledges)

Scree or talus slope parameters
(from the valley floor to the base of the nest cliff)

HTSC	Vertical height (1:50 000 topographical maps; m)
LTSC	Horizontal length (1:50 000 topographical maps; m)
ANSC	Average angle of the slope (Tan^{-1}(HTSC/LTSC); degrees)
HETIN	Heterogeneity index (coefficient of variation of canopy closure, see methods)
REFIN	Refuge index (canopy closure or 100%-canopy closure, see methods)
LUSC	Land use: (1) nature reserve (2) unused (3) livestock (4) forestry/plantations (5) agriculture (6) suburban/urban (categories 1–6 in possible order of increasing potential for disturbance)
WTVA	Width of valley: (1) >5 km (2) 1–5 km (3) <1 km (categories 1–3 in order of decreasing valley width)

Appendix 2 continued...

Location	
TOTEL	Total elevation above the valley floor (HTCL + HTSC; m)
WDIR	Prevailing wind direction in the breeding season, relative to ASCL: (1) same sector to (5) opposite sector (categories 1–5 in order of decreasing exposure of the nest cliff to wind)
NFWB	Distance to the nearest obvious, permanent source of fresh water (1:50 000 topographical maps; km)
NHS	Distance to the nearest established village or town (1:50 000 topographical maps; km)
NAGR	Distance to the nearest agricultural fields (1:50 000 topographical maps; km)

Immature Lanner Falcon ♀
Nossob water hole
ten past nine, Tuesday 12th August 1977
morning

Appendix 3 Nesting habitat characteristics of Peregrines in subtropical and south temperate areas of South Africa. Data for numerical variables are means ± SD, with F *values from one-way ANOVA. For categorial variables, χ^2 values compare frequency distributions, and categories used relatively more by one population than the other are listed with adjusted residuals in parentheses. Only statistically significant results are shown,* *P<*0.05;* **P<*0.01;* ***P<*0.001*

variable	subtropical	temperate	test statistic
Study area nest sites (Soutpansberg $n = 22$, Cape Peninsula $n = 30$)			
LTFL (cm)	461 ± 276	305 ± 244	4.64*
ASST[a]	1 (4.4***)	4 (3.2**)	31.30***
AASL (m)	1422 ± 163	257 ± 202	492.50***
HTCL (cm)	111 ± 35	85 ± 52	18.70***
LTCL (m)	566 ± 228	279 ± 262	17.02***
ACL (m^2)	61886 ± 32685	24278 ± 32428	16.96***
VERC[a]	3 (3.2**)	2 (2.1*)	12.50*
TPCL[a]	4 (3.6***)	1 (2.2*)	21.50***
STFC[a]	2 (5.5***)	1 (2.6**)	30.20***
HTSC (m)	375 ± 208	182 ± 189	12.95**
LTSC (m)	3014 ± 1090	918 ± 1027	50.13***
ANSC (°)	6.9 ± 1.6	13.2 ± 12.6	5.43*
REFIN	20.1 ± 8.8	13.3 ± 10.6	6.00*
LUSC[a]	3 (4.6***)	1 (3.0**)	39.30***
WTVA[a]	2 (2.1*)	1 (2.1*)	4.30*
TOTEL (m)	486 ± 203	270 ± 209	13.84**
WDIR[a]	3 (3.6***)	2 (2.2*)	14.90**
NFWB (km)	12.3 ± 10.3	2.1 ± 1.6	28.24***
NHS (km)	31.5 ± 22.8	1.5 ± 2.2	51.58***
NAGR (km)	1.5 ± 1.3	6.0 ± 3.9	27.14***
All nest sites (subtropical $n = 18$–19, temperate $n = 23$–26)			
ASST[a]	1 (2.4*)	4 (2.7**)	17.60*
AASL (m)	1397 ± 157	294 ± 216	356.54***
HTCL (m)	122 ± 37	86 ± 54	6.34*
LTCL (m)	573 ± 255	310 ± 274	10.82**
VERC[a]	3 (3.2*)	2 (2.1*)	12.50*
ACL (m^2)	70500 ± 37308	27642 ± 34312	15.91**
TPCL[a]	4 (3.6***)	5 (2.7***)	21.50***
STFC[a]	2 (3.9***)	1 (2.1*)	15.80**
HTSC (m)	331 ± 176	199 ± 181	5.95*
LTSC (m)	2792 ± 1617	917 ± 1065	21.99***
REFIN	21.0 ± 8.9	12.1 ± 9.8	9.06**
LUSC[a]	3 (4.7***)	1 (2.9**)	29.10***
TOTEL (m)	453 ± 195	289 ± 219	6.75*
WDIR	3 (3.6***)	2 (2.2*)	14.90***
NFWB (km)	13.5 ± 10.7	2.3 ± 1.6	27.75***
NHS (km)	39.5 ± 19.0	3.7 ± 6.0	81.57***
NAGR (km)	2.1 ± 1.6	5.4 ± 3.8	13.11***
All cliffs (subtropical $n = 20$, temperate $n = 20$)			
HTCL (m)	144 ± 78	100 ± 60	4.12*
LTSC (m)	3045 ± 2535	1215 ± 1304	8.88*
LUSC[a]	3 (3.0**)	-	13.60*
NFWB (km)	6.8 ± 8.7	2.7 ± 2.4	4.54*
NHS (km)	28.6 ± 15.8	8.9 ± 11.9	20.37**

[a] categorial variables

Appendix 4 *Characteristics of Peregrine and Lanner nesting habitats in South Africa. Data for numerical variables are means ± SD, with* F *values from one-way ANOVA. For categorial variables, χ^2 values compare frequency distributions, and categories used relatively more by one species than the other are listed with adjusted residuals in parentheses. Only statistically significant results are shown,* *$P<0.05$, **$P<0.01$, ***$P<0.001$

variable	Peregrines	Lanners	test statistic
Soutpansberg nest sites (Peregrines $n = 22$, Lanners $n = 23–24$)			
LTFL (cm)	461 ± 276	146 ± 73	29.11***
WTFL (cm)	123 ± 45	77 ± 52	10.52**
AFLO (m^2)	6.24 ± 5.23	1.34 ± 1.79	18.70***
TPST^a	3 (3.0**)	2 (2.1*)	10.60*
VERC^a	4 (2.2*)	3 (2.6**)	10.50*
TPCL^a	4 (3.3***)	3 (2.1*)	13.20**
ANSC (°)	6.9 ± 1.6	9.4 ± 3.5	9.63**
HETIN	0.199 ± 0.108	0.111 ± 0.048	12.74***
REFIN	20.1 ± 8.8	12.8 ± 4.6	12.22**
LUSC^a	4 (3.3***)	5 (3.4***)	20.60***
All nest sites (Peregrines $n = 52$, Lanners $n = 23$)			
LTFL (cm)	339 ± 244	164 ± 97	10.93**
WTFL (cm)	135 ± 78	81 ± 53	8.82**
AENT (m^2)	6.42 ± 10.10	1.80 ± 2.24	4.68*
AFLO (m^2)	5.21 ± 5.83	1.55 ± 1.92	8.57**
AASL (m)	708 ± 560	1286 ± 322	21.27***
VERC^a	5 (2.3*)	4 (3.1**)	15.30**
LUSC^a	2 (2.1*)	5 (4.0***)	23.30***
WTVA^a	1 (2.0*)	2 (3.1**)	9.50**
NAGR (km)	4.0 ± 3.3	2.3 ± 1.9	4.97*
All cliffs (Peregrines $n = 48–57$, Lanners $n = 74–76$)			
HTCL (m)	138 ± 111	78 ± 40	18.69***
VERC^a	5 (3.5***)	-	13.60**
ACL (m^2)	71045 ± 103881	32016 ± 28763	9.60**
TPCL^a	4 (2.3*)	-	11.90*
STFC^a	-	3 (3.4***)	12.50*
HTSC (m)	348 ± 380	212 ± 191	7.31**
LTSC (m)	2162 ± 2763	1209 ± 1440	6.54*
LUSC^a	1 (4.1***)	5 (4.0***)	39.80***
WTVA^a	1 (4.2***)	2 (2.8**)	18.40**
TOTEL (m)	509 ± 478	289 ± 206	12.80**
NAGR (km)	5.1 ± 5.3	1.5 ± 1.6	30.83***

^{a}categorial variables

Appendix 5. *Comparative morphometric data for southern African Peregrines and Lanners. Data for adults and immatures were pooled, except where these were significantly different, when only adults were compared. Data given are means ± SD (n.s. = not significant,* *P<*0.05,* **P<*0.01,* ***P<*0.001)*

	Peregrine males (*n*)	Lanner males (*n*)	*t* value	Peregrine females (*n*)	Lanner females (*n*)	*t* value
body mass (kg)	0.53 ± 0.03 (13)	0.51 ± 0.04 (20)	2.01 n.s.	0.77 ± 0.07 (20)	0.73 ± 0.06 (21)	2.13*
body length (mm)	360 ± 11 (11)	390 ± 11 (19)	6.98***	403 ± 11 (15)	444 ± 16 (20)	8.44***
bill length (mm)	19.5 ± 1.0 (11)	19.3 ± 1.0 (20)	0.52 n.s.	22.7 ± 1.0 (11)	22.3 ± 1.5 (9)	0.84 n.s.
bill width (mm)	15.5 ± 1.8 (11)	15.2 ± 1.9 (20)	0.43 n.s.	15.2 ± 1.2 (11)	16.5 ± 0.7 (9)	1.90 n.s.
bill depth (mm)	14.4 ± 0.5 (11)	14.7 ± 0.5 (20)	1.63 n.s.	16.5 ± 0.5 (16)	16.2 ± 0.7 (21)	1.68 n.s.
wing span (m)	0.87 ± 0.02 (13)	0.96 ± 0.03 (20)	9.17***	0.98 ± 0.05 (20)	1.07 ± 0.04 (21)	6.52***
wing length (mm)	284 ± 7 (11)	315 ± 11 (19)	8.31***	321 ± 7 (16)	354 ± 10 (21)	11.27***
wing area (m^2)	0.09 ± 0.01 (13)	0.12 ± 0.01 (20)	6.85***	0.12 ± 0.01 (20)	0.15 ± 0.01 (21)	10.31***
ulna length (mm)	80 ± 6 (11)	90 ± 5 (20)	5.08***	95 ± 6 (16)	98 ± 5 (21)	1.75 n.s.
secondary length (mm)	129 ± 8 (11)	156 ± 5 (20)	12.27***	149 ± 4 (11)	177 ± 7 (9)	8.07***
outer rectrix length (mm)	132 ± 6 (6)	159 ± 5 (7)	9.24***	152 ± 5 (10)	183 ± 6 (9)	8.88***
inner rectrix length (mm)	138 ± 7 (11)	165 ± 7 (20)	10.04***	153 ± 6 (15)	189 ± 9 (21)	13.57***
tarsus length (mm)	45.4 ± 4.5 (11)	48.3 ± 3.7 (20)	1.94 n.s.	53.0 ± 3.2 (16)	52.2 ± 3.8 (21)	0.71 n.s.
tarsus width (mm)	6.1 ± 0.3 (11)	6.0 ± 0.3 (20)	0.79 n.s.	7.2 ± 0.4 (16)	6.8 ± 0.4 (21)	3.23**
toe 1 length (mm)	27.3 ± 3.9 (11)	25.7 ± 3.2 (20)	1.23 n.s.	32.0 ± 3.3 (15)	25.8 ± 4.0 (21)	4.92***
toe 2 length (mm)	46.4 ± 2.8 (11)	43.4 ± 2.1 (20)	3.40**	51.1 ± 3.0 (15)	45.3 ± 2.8 (21)	5.94***
toe 3 length (mm)	34.0 ± 3.3 (11)	29.2 ± 3.3 (20)	3.85***	37.7 ± 3.5 (15)	32.0 ± 3.5 (21)	4.83***
toe 4 length (mm)	23.2 ± 2.9 (11)	20.4 ± 2.3 (20)	2.96**	26.1 ± 3.0 (15)	22.3 ± 1.6 (21)	5.09***
claw 1 length (mm)	18.6 ± 0.9 (10)	16.7 ± 1.3 (20)	4.24***	21.2 ± 1.2 (15)	18.5 ± 1.0 (21)	7.36***
claw 2 length (mm)	17.4 ± 0.9 (10)	16.2 ± 0.6 (20)	4.30***	20.1 ± 1.1 (15)	18.6 ± 1.3 (21)	3.10*

Appendix 5 continued...

claw 3 length (mm)	16.3 ± 0.9 (10)	15.2 ± 0.9 (20)	3.22**	19.9 ± 5.9 (15)	16.5 ± 1.1 (21)	2.64*
claw 4 length (mm)	19.6 ± 0.9 (10)	18.3 ± 0.8 (20)	4.33***	22.9 ± 1.9 (15)	20.0 ± 1.0 (21)	6.04***
wing loading (Nm^{-2})	57.2 ± 4.3 (13)	42.1 ± 3.9 (20)	10.38***	63.3 ± 3.9 (20)	49.1 ± 4.4 (21)	10.96***
aspect ratio	8.49 ± 0.37 (11)	7.92 ± 0.42 (20)	3.77***	8.18 ± 0.56 (16)	7.83 ± 0.54 (21)	1.95 n.s.

Appendix 6 Invertebrate and vertebrate taxa identified from remains collected at falcon nest sites in South Africa. Remains were collected at 10 Peregrine sites on the Cape Peninsula, seven Peregrine sites on the Orange River and seven Peregrine sites and nine Lanner sites in the Soutpansberg. Data provided are the average mass of each taxon and the number of individuals identified, with the number of nest sites at which each taxon was collected in parentheses. Items marked with an asterisk were not considered as falcon prey in the diet analyses

Prey taxon	average mass (g)	Cape Peninsula	Orange River	Soutpansberg	
				Peregrines	Lanners
CLASS: INSECTA		-	**2(1)**	**14(2)**	**3(2)**
Order: Orthoptera		-	**1(1)**	**12(2)**	**3(2)**
unidentified orthopteran	3	-	1(1)	12(2)	3(2)
Order: Coleoptera		-	**1(1)**	**2(1)**	-
unidentified coleopteran	3	-	1(1)	2(1)	-
CLASS: AMPHIBIA		-	-	***2(1)**	-
unidentified frog	20	-	-	*2(1)	-
CLASS: AVES		**512(10)**	**224(7)**	**385(7)**	**169(9)**
Family: Accipitridae		-	-	**1(1)**	-
Little Sparrowhawk – male *Accipiter minullus*	80	-	-	1(1)	-
Family: Falconidae		-	-	***2(2)**	***1(1)**
Peregrine Falcon – nestling	250	-	-	*2(2)	-
Lanner Falcon – nestling	250	-	-	-	*1(1)
Family: Phasianidae		**1(1)**	**1(1)**	**6(3)**	**70(8)**
Coqui Francolin *Francolinus coqui*	230	-	-	1(1)	-
Crested Francolin *F. sephaena*	340	-	-	2(1)	1(1)
Greywing Francolin *F. africanus*	390	1(1)	-	-	-
Cape Francolin – pullus *F. capensis*	150	-	1(1)	-	-
Natal Francolin – female *F. natalensis*	425	-	-	2(2)	-
Natal Francolin – unsexed	520	-	-	-	1(1)
unidentified *Francolinus* sp. – adult	500	-	-	-	2(2)
unidentified *Francolinus* sp. – pullus	150	-	-	-	1(1)
Domestic Chicken <3 days old *Gallus gallus*	60	-	-	-	41(8)
Domestic Chicken ±7 days old	150	-	-	-	23(3)
Domestic Chicken ±14 days old	250	-	-	-	1(1)
Harlequin Quail *C. delegorguei*	65	-	-	1(1)	-

Appendix 6 continued...

Family: Charadriidae		**5(3)**	**-**	**16(5)**	**16(6)**
Whitefronted Plover *Charadrius marginatus*	49	2(2)	-	-	-
Kittlitz Plover *C. pecuarius*	43	2(1)	-	-	-
Crowned Plover – adult *Vanellus coronatus*	167	1(1)	-	16(5)	14(6)
Crowned Plover – immature	167	-	-	-	2(2)
Family: Scolopacidae		**3(1)**	**2(2)**	**-**	**1(1)**
Greenshank *Tringa nebularia*	191	-	1(1)	-	1(1)
Curlew Sandpiper *Calidris ferruginea*	57	3(1)	-	-	-
Little Stint *C. minuta*	24	-	1(1)	-	-
Family: Recurvirostridae		**-**	**-**	**2(1)**	**2(2)**
Blackwinged Stilt *Himantopus himantopus*	175	-	-	2(1)	2(2)
Family: Glareolidae		**-**	**-**	**4(3)**	**-**
Temminck's Courser *Cursorius temminckii*	74	-	-	4(3)	-
Family: Laridae		**2(1)**	**6(3)**	**-**	**-**
Common Tern *Sterna hirundo*	124	2(1)	3(1)	-	-
Whitewinged Tern *Chlidonias leucopterus*	57	-	1(1)	-	-
unidentified *Sterna* sp.	100	-	2(2)	-	-
Family: Pteroclidae		**-**	**24(6)**	**4(2)**	**-**
Namaqua Sandgrouse *Pterocles namaqua*	185	-	24(6)	-	-
Burchell's Sandrouse *P. burchelli*	235	-	-	1(1)	-
Doublebanded Sandgrouse *P. bicinctus*	235	-	-	3(2)	-
Family: Columbidae		**339(10)**	**93(6)**	**196(7)**	**49(8)**
Feral or Domestic Pigeon – adult *Columba livia*	320	47(7)	8(4)	17(3)	-
Feral or Domestic Pigeon – fledgling	320	1(1)	-	-	-
Rock Pigeon - adult *C. guinea*	347	28(7)	35(6)	20(5)	6(2)
Rock Pigeon – fledgling	347	8(3)	2(2)	1(1)	1(1)
Rameron Pigeon *C. arquatrix*	415	-	-	2(2)	-
unidentified *Columba* sp. – adult	330	1(1)	-	-	-
unidentified *Columba* sp. – fledgling	330	2(2)	-	-	-

Appendix 6 continued...

Redeyed Dove – adult *Streptopelia semitorquata*	235	40(7)	16(5)	34(6)	10(4)
Redeyed Dove – fledgling	235	1(1)	-	-	-
Cape Turtle Dove *S. capicola*	153	61(7)	5(4)	25(5)	8(5)
Laughing Dove – adult *S. senegalensis*	102	140(8)	20(5)	79(7)	21(7)
Laughing Dove – fledgling	102	4(2)	-	-	2(2)
unidentified *Streptopelia* sp. – fledgling	130	3(3)	-	-	-
Namaqua Dove *Oena capensis*	40	3(3)	7(5)	15(5)	-
Greenspotted Dove *Turtur chalcospilos*	65	-	-	1(1)	1(1)
small unidentified columbid	50	-	-	1(1)	-
medium unidentified columbid	160	-	-	1(1)	-
Family: Psittacidae		**5(2)**	-	**1(1)**	-
Cockatiel *Nymphicus hollandicus*	90	1(1)	-	-	-
Budgerigar *Melopsittacus undulatus*	28	4(1)	-	1(1)	-
Family: Musophagidae		-	-	**1(1)**	-
Grey Loerie *Corythaixoides concolor*	269	-	-	1(1)	-
Family: Caprimulgidae		-	**2(1)**	**1(1)**	-
Freckled Nightjar *Caprimulgus tristigma*	60	-	2(1)	-	-
unidentified nightjar sp.	60	-	-	1(1)	-
Family: Apodidae		**32(8)**	**25(7)**	**25(5)**	**2(2)**
Black Swift – adult *Apus barbatus*	45	13(5)	-	12(3)	-
Black Swift – fledgling	45	1(1)	-	-	-
Bradfield's Swift *A. bradfieldii*	45	-	18(6)	-	-
Little Swift *A. affinis*	26	12(3)	-	2(2)	-
Alpine Swift *A. melba*	77	6(4)	6(5)	11(3)	2(2)
unidentified *Apus* sp.	35	-	1(1)	-	-
Family: Coliidae		**5(3)**	**3(3)**	**55(7)**	**1(1)**
Speckled Mousebird *Colius striatus*	53	-	-	14(6)	1(1)
Whitebacked Mousebird – adult *C. colius*	41	1(1)	2(2)	-	-
Whitebacked Mousebird – fledgling	41	-	1(1)	-	-
Redfaced Mousebird *Urocolius indicus*	56	4(3)	-	41(7)	-

Appendix 6 continued...

Family: Trogonidae		-	-	**1(1)**	-
Narina Trogon *Apaloderma narina*	65	-	-	1(1)	-
Family: Alcedinidae		-	**1(1)**	-	-
Pied Kingfisher *Ceryle rudis*	82	-	1(1)	-	-
Family: Meropidae		-	-	**1(1)**	-
European Bee-eater *Merops apiaster*	55	-	-	1(1)	-
Family: Upupidae		-	**1(1)**	**1(1)**	-
Hoopoe *Upupa epops*	57	-	1(1)	1(1)	-
Family: Phoeniculidae		-	**1(1)**	-	-
Scimitarbilled Woodhoopoe *Phoeniculus cyanomelas*	35	-	1(1)	-	-
Family: Bucerotidae		-	-	-	**1(1)**
Redbilled Hornbill *Tockus erythrorhynchus*	130	-	-	-	1(1)
Family: Capitonidae		-	-	**2(2)**	-
Blackcollared Barbet *Lybius torquatus*	57	-	-	2(2)	-
Family: Alaudidae		-	**19(1)**	**4(2)**	**1(1)**
Redcapped Lark *Calandrella cinerea*	26	-	-	1(1)	-
Chestnutbacked Finchlark *Eremopterix leucotis*	14	-	-	1(1)	1(1)
Greybacked Finchlark *E. verticalis*	17	-	19(1)	-	-
unidentified lark sp.	20	-	-	2(1)	-
Family: Hirundinidae		**2(2)**	**15(5)**	-	-
European Swallow *Hirundo rustica*	18	1(1)	-	-	-
Rock Martin *H. fuligula*	22	1(1)	4(4)	-	-
Brownthroated Martin *Riparia paludicola*	13	-	11(3)	-	-
Family: Oriolidae		-	-	**1(1)**	-
Blackheaded Oriole *Oriolus larvatus*	69	-	-	1(1)	-
Family: Sylviidae		-	**2(2)**	-	-
unidentified sylviid	20	-	2(2)	-	-
Family: Laniidae		-	**1(1)**	**1(1)**	-
Fiscal Shrike *Lanius collaris*	41	-	-	1(1)	-
unidentified shrike sp.	60	-	1(1)	-	-

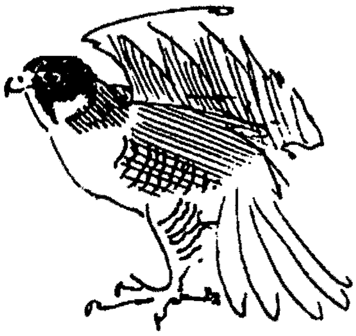
Appendix 6 continued...

Family: Sturnidae		**77(9)**	**4(2)**	**13(5)**	**1(1)**
European Starling – adult *Sturnus vulgaris*	76	68(9)	-	-	-
European Starling – fledgling	76	5(3)	-	-	-
Pied Starling *Spreo bicolor*	107	1(1)	-	-	-
Plumcoloured Starling *Cinnyricinclus leucogaster*	46	-	-	1(1)	-
Cape Glossy Starling *Lamprotornis nitens*	84	-	-	6(3)	-
Greater Blue-eared Glossy Starling *L. chalybaeus*	76	-	-	1(1)	-
unidentified *Lamprotornis* sp.	80	-	-	2(1)	-
Redwinged Starling – adult *Onychognathus morio*	135	3(3)	-	1(1)	-
Redwinged Starling – fledgling	135	-	-	1(1)	-
Palewinged Starling *O. nabouroup*	107	-	4(2)	-	-
unidentified starling sp.	80	-	-	1(1)	1(1)
Family: Ploceidae		**23(4)**	**11(5)**	**17(5)**	**8(6)**
Whitebrowed Sparrow-weaver *Plocepasser mahali*	48	-	-	3(3)	1(1)
Sociable Weaver *Philetairus socius*	27	-	1(1)	-	-
House Sparrow *Passer domesticus*	24	2(1)	-	-	-
Cape Sparrow *P. melanurus*	26	10(3)	4(3)	4(3)	2(2)
Cape Weaver *Ploceus capensis*	45	7(4)	-	3(2)	-
Masked Weaver *P. velatus*	27	1(1)	1(1)	-	1(1)
unidentified *Ploceus* sp.	35	-	-	1(1)	1(1)
Redbilled Quelea *Quelea quelea*	19	-	2(2)	6(3)	1(1)
Red Bishop *Euplectes orix*	23	-	2(2)	1(1)	-
Yellowrumped Widow *E. capensis*	45	2(1)	-	-	-
unidentified ploceid	40	1(1)	1(1)	-	2(2)
Family: Estrildidae		-	**3(3)**	**3(3)**	-
Common Waxbill *Estrilda astrild*	8	-	3(3)	-	-
Redheaded Finch *Amadina erythrocephalus*	23	-	-	3(3)	-
Family: Fringillidae		**2(1)**	**4(2)**	**4(2)**	**2(2)**
Yelloweyed Canary *Serinus mozambicus*	13	-	-	1(1)	-
Forest Canary *S. scotops*	16	-	-	1(1)	-
Bully Canary *S. sulphuratus*	26	-	-	-	1(1)

Appendix 6 continued...

Yellow Canary *S. flaviventris*	17	1(1)	1(1)	-	-
Whitethroated Canary *S. albogularis*	27	-	2(1)	-	-
unidentified *Serinus* sp.	15	1(1)	-	1(1)	-
unidentified fringillid	15	-	1(1)	1(1)	1(1)
unidentified small birds – adult	**20**	**4(3)**	**2(2)**	**9(3)**	**2(2)**
unidentified small birds – fledgling	**20**	**1(1)**	**-**	**-**	**-**
unidentified small-medium birds – adult	**60**	**5(3)**	**-**	**11(4)**	**8(6)**
unidentified small-medium birds – fledgling	**60**	**1(1)**	**-**	**-**	**-**
unidentified medium birds – adult	**130**	**-**	**-**	**1(1)**	**-**
unidentified medium birds – fledgling	**130**	**5(3)**	**4(4)**	**1(1)**	**4(2)**
unidentified very large birds	**600**	**-**	**-**	**1(1)**	**-**
CLASS: MAMMALIA		**3(3)**	**26(6)**	**17(5)**	**3(1)**
Family: Soricidae		**-**	**-**	**-**	**1(1)**
unidentified shrew	10	-	-	-	1(1)
Family: Pteropodidae		**-**	**-**	**6(2)**	**-**
unidentified fruit bat	130	-	-	6(2)	-
Family: Molossidae			**16(1)**	**-**	**-**
Flat-headed Free-tailed bat *Sauromys petrophilus*	14	-	8(1)	-	-
Egyptian Free-tailed bat *Tadarida aegyptiaca*	15	-	8(1)	-	-
Family: Rhinolophidae		**-**	**-**	**1(1)**	**-**
Hildebrandt's Horseshoe Bat *Rhinolophus hildebrantii*	30	-	-	1(1)	-
unidentified insectivorous bats	**15**	**1(1)**	**6(4)**	**3(3)**	**-**
Family: Muridae		***2(2)**	***4(4)**	***5(2)**	**2(1)**
Multimammate Mouse *Mastomys natalensis*	65	-	-	*1(1)	-
Namaqua Rock Mouse *Aethomys namaquensis*	45	-	*1(1)	-	-
small unidentified murid	25	-	-	-	1(1)
medium unidentified murid	45	*2(2)	*3(3)	*2(2)	1(1)
large unidentified murid	120	-	-	*2(2)	-

Family: Sciuridae		-	-	***1**(1)	-
unidentified squirrel	160	-	-	***1**(1)	-
Family: Bovidae		-	-	***1**(1)	-
small unidentified bovid	5000	-	-	***1**(1)	-
TOTAL		**515**(10)	**252**(7)	**418**(7)	**175**(10)

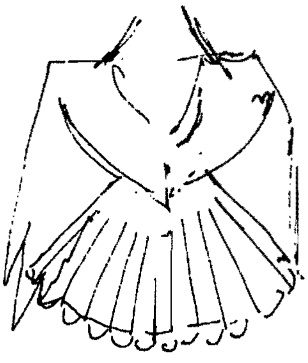


***Appendix** 7 Taxa observed as prey of breeding Peregrines in South Africa. Prey were identified at 12 nest sites on the Cape Peninsula, five nest sites on the Orange River and five nest sites in the Soutpansberg. Data provided are the average mass of each taxon and the number of individuals observed as prey, with the number of sites at which each prey taxon was observed in parentheses*

Prey taxon	average mass (g)	Cape Peninsula	Orange River	Soutpansberg
CLASS: AVES		**159(12)**	**78(5)**	**56(5)**
Family: Columbidae		**52(11)**	**17(5)**	**8(2)**
Feral or Domestic Pigeon	320	9(6)	-	-
Rock Pigeon – adult	347	3(2)	6(2)	-
Rock Pigeon – nestling	347	-	2(1)	-
unidentified *Columba* sp.	330	5(2)	-	-
Cape Turtle Dove	153	2(2)	1(1)	-
Laughing Dove	102	5(3)	-	-
unidentified *Streptopelia* sp.	130	28(7)	6(4)	8(2)
Namaqua Dove	40	-	2(2)	-
Family: Apodidae		**17(7)**	**13(4)**	**-**
Black Swift	45	7(3)	-	-
Little Swift	26	2(1)	-	-
Alpine Swift	77	1(1)	12(3)	-
unidentified *Apus* sp.	35	7(5)	1(1)	-
Family: Coliidae		**1(1)**	**1(1)**	**-**
Redfaced Mousebird *Urocolius indicus*	56	1(1)	1(1)	-
Family: Hirundinidae		**1(1)**	**7(1)**	**-**
European Swallow	18	-	3(1)	-
Rock Martin	22	1(1)	1(1)	-
unidentified *Hirundo* sp.	20	-	1(1)	-
unidentified hirundinid	15	-	2(1)	-
Family: Pycnonotidae		**-**	**-**	**1(1)**
Blackeyed Bulbul *Pycnonotus barbatus*	37	-	-	1(1)
Family: Sylviidae		**1(1)**	**-**	**-**
unidentified *prinia* sp.	9	1(1)	-	-
Family: Sturnidae		**4(3)**	-	-
European Starling – adult	76	1(1)	-	-
European Starling – fledgling	76	2(1)	-	-
Redwinged Starling – nestling	135	1(1)	-	-
Family: Ploceidae		**-**	**16(1)**	**-**
unidentified *Ploceus* sp.	35	-	1(1)	-

Appendix 7 continued...

Redbilled Quelea	19	-	15(1)	-
unidentified ploceid	40	-	-	-
unidentified small birds	**20**	**24(4)**	**15(4)**	**12(4)**
unidentified small-medium birds	**60**	**47(7)**	**3(3)**	**20(5)**
unidentified medium birds	**130**	**12(6)**	**4(4)**	**13(5)**
unidentified medium-large birds	**220**	**-**	**1(1)**	**-**
unidentified large birds	**350**	**-**	**-**	**2(2)**
CLASS: MAMMALIA		**-**	**3(2)**	**-**
unidentified insectivorous bat	**15**	**-**	**3(2)**	**-**
TOTAL		**159(12)**	**81(5)**	**56(5)**



***Appendix 8** List of the bird species recorded on 1 km line-transects walked in seven habitats in the Soutpansberg, with the average number of individuals of each species counted per transect in each habitat. Habitats are (SW) savanna woodland, (DW) denuded woodland, (FP) forest & plantation, (GF) grassland & scrub forest, (MT) moist thornscrub, (DE) deciduous woodland, (DT) dry thornscrub. Between nine and 12 transects were walked in each habitat*

Species counted	SW	DW	FP	GF	MT	DE	DT
Redbreasted Sparrowhawk *Accipiter rufiventris*	-	-	-	0.1	-	-	-
Rock Kestrel	-	0.1	-	-	-	-	-
Crested Francolin	0.2	-	-	-	-	-	-
Natal Francolin	0.3	-	-	-	-	-	-
Swainson's Francolin *Francolinus swainsonii*	0.8	-	-	-	-	-	-
unidentified *Francolinus* sp.	-	-	-	0.1	-	0.1	-
Crowned Plover	-	0.6	-	-	-	-	-
Temminck's Courser	-	0.4	-	-	-	-	-
Rameron Pigeon	-	-	-	0.2	-	-	-
Cape Turtle Dove	0.6	-	-	-	-	-	-
Laughing Dove	1.2	-	-	-	-	-	-
Greenspotted Dove	0.3	-	0.1	-	-	0.7	0.1
Tambourine Dove *Turtur tympanistria*	-	-	0.1	-	-	-	-
unidentified dove sp.	-	-	0.2	-	-	-	-
Knysna Loerie *Tauraco corythaix*	-	-	0.1	-	-	-	-
Purplecrested Loerie *Tauraco porphyreolophus*	-	-	0.1	-	-	-	-
Speckled Mousebird	-	-	-	0.4	-	-	-
Brownhooded Kingfisher *Halcyon albiventris*	0.3	-	-	-	-	-	0.1
Striped Kingfisher *H. chelicuti*	0.1	-	-	-	-	-	-
Yellowbilled Hornbill *Tockus flavirostris*	0.2	-	-	-	-	-	-
Blackcollared Barbet	0.1	-	-	-	-	-	0.1
Yellowfronted Tinkerbarbet *Pogoniulus chrysoconus*	-	-	-	-	-	-	0.1
Cardinal Woodpecker *Dendropicos fuscescens*	0.1	-	-	-	-	-	-
Olive Woodpecker *Mesopicos griseocephalus*	-	-	-	0.1	-	-	-
unidentified lark sp.	-	0.2	-	0.1	-	0.2	-
Chestnutbacked Finchlark	-	13.6	-	-	-	-	-
Redbreasted Swallow *Hirundo semirufa*	-	0.2	-	-	-	-	-
Blackheaded Oriole	-	-	0.1	-	-	-	-
Southern Black Tit *Parus niger*	0.1	-	-	-	-	-	0.3

Appendix 8 continued...

Blackeyed Bulbul	0.9	-	0.8	1.6	0.2	1.0	0.5
Terrestrial Bulbul *Phyllastrephus terrestris*	-	-	0.1	-	0.2	-	-
Sombre Bulbul *Andropadus importunus*	-	-	0.3	0.1	-	-	-
Olive Thrush *Turdus olivaceus*	-	-	0.2	-	0.1	-	-
Cape Rock Thrush *Monticola rupestris*	-	-	-	-	-	0.4	-
Familiar Chat *Cercomela familiaris*	-	-	-	0.5	-	0.4	-
Heuglin's Robin *Cossypha heuglini*	-	-	0.1	-	-	-	-
Cape Robin *Cossypha caffra*	-	-	0.2	0.2	-	-	-
Whitebrowed Robin *Erythropygia leucophyrs*	0.1	-	-	-	-	-	-
Titbabbler *Parisoma subcaeruleum*	-	0.2	-	-	-	-	-
Barthroated Apalis *Apalis thoracica*	-	-	0.1	0.3	-	0.1	-
Yellowbreasted Apalis *Apalis flavida*	0.3	-	-	-	-	-	-
Longbilled Crombec *Sylvietta rufescens*	-	0.1	-	-	-	-	-
Lazy Cisticola *Cisticola aberrans*	-	-	-	-	-	0.1	-
unidentified *Cisticola* sp.	0.5	-	-	0.8	0.2	0.7	0.1
Tawnyflanked Prinia *Prinia subflava*	-	-	-	0.2	-	-	-
Blackchested Prinia *Prinia flavicans*	-	0.7	-	-	-	-	-
Dusky Flycatcher *Muscicapa adusta*	-	-	0.2	-	-	-	-
Cape Batis *Batis capensis*	-	-	1.0	0.3	-	-	-
Chinspot Batis *Batis molitor*	0.4	-	-	-	-	0.1	-
Fairy Flycatcher *Stenostira scita*	0.1	-	-	-	-	-	-
Striped Pipit *Anthus lineiventris*	0.1	-	-	-	0.1	-	-
unidentified pipit sp.	-	0.1	0.1	0.1	-	-	-
Fiscal Shrike	0.4	0.2	-	-	-	-	-
Southern Boubou *Laniarius ferrugineus*	-	-	-	-	0.1	-	-
Puffback *Dryoscopus cubla*	0.1	-	-	-	-	-	0.1
Threestreaked Tchagra *Tchagra australis*	0.1	-	-	-	-	-	-
Gurney's Sugarbird *Promerops gurneyi*	-	-	-	0.3	-	0.7	-

Appendix 8 continued...

Greater Doublecollared Sunbird *Nectarina afra*	-	-	-	0.5	0.4	-	-
Whitebellied Sunbird *N. talatala*	0.8	0.2	-	-	-	-	0.6
Scarletchested Sunbird *N. senegalensis*	0.1	-	-	-	-	-	-
Black Sunbird *N. amethystina*	0.2	-	-	0.1	-	-	-
Cape Whiteye *Zosterops pallidus*	-	-	-	0.8	0.2	0.3	0.5
Whitebrowed Sparrow-weaver	0.3	3.0	-	-	-	-	-
Great Sparrow *Passer motitensis*	-	0.1	-	-	-	-	-
Cape Sparrow	-	4.3	-	-	-	-	-
Greyheaded Sparrow *P. griseus*	0.2	-	-	-	-	-	-
Scalyfeathered Finch *Sporopipes squamifrons*	-	0.8	-	-	-	-	-
Spectacled Weaver *Ploceus ocularis*	-	0.8	-	-	-	-	-
Masked Weaver	-	0.1	-	-	-	-	-
Yellowrumped Widow	0.7	-	-	-	-	-	-
Melba Finch *Pytilia melba*	1.5	-	-	-	-	-	-
Bluebilled Firefinch *Lagonosticta rubricata*	0.8	-	0.2	-	-	-	-
Jameson's Firefinch *L. rhodopareia*	0.1	-	-	-	-	-	-
unidentified *Lagonosticta* sp.	-	-	0.1	-	-	-	-
Blue Waxbill	8.5	-	-	-	-	-	-
Common Waxbill	0.1	-	-	-	-	-	-
Swee Waxbill *Estrilda melanotis*	-	-	0.6	-	-	-	1.0
Redheaded Finch	-	4.3	-	-	-	-	-
Yelloweyed Canary	0.2	-	-	-	-	-	1.0
Cape Canary *Serinus canicollis*	-	-	-	0.2	-	-	-
Bully Canary	-	-	-	0.1	-	-	-
Streakyheaded Canary *S. gularis*	-	-	-	-	-	0.8	-
unidentified *Serinus* sp.	0.1	0.1	-	0.2	-	-	-
Cape Bunting *E. capensis*	-	-	-	0.1	-	-	-
unidentified small bird	-	0.3	0.1	-	-	-	-
unidentified small-medium bird	0.8	0.7	0.1	0.1	0.2	0.1	-
unidentified medium bird	-	-	0.1	-	-	-	-

Appendix 9 *Territory occupancy and the frequency of breeding and successful breeding by Peregrines and Lanners in three areas of South Africa in each year of the study*

population/ year	number of occupied territories[a]	number of breeding pairs[b]	number of successful pairs[c]
Peregrines			
Cape Peninsula			
1989	5 (100)	1 (20)	1 (20)
1990	9 (100)	5 (56)	4 (44)
1991	8 (89)	3 (38)	2 (25)
1992	12 (100)	6 (50)	6 (50)
1993	12 (92)	7 (58)	7 (58)
1994	12 (92)	11 (92)	9 (75)
1995	15 (94)	13 (80)	7 (47)
1996	15 (88)	9 (60)	3 (20)
1997	16 (94)	16 (100)	15 (94)
Orange River			
1989[d]	4 (100)	4 (100)	4 (100)
1990	5 (100)	5 (100)	5 (100)
1991[d]	6 (100)	5 (83)	5 (83)
1992[d]	5 (83)	4 (80)	4 (80)
1993[d]	6 (86)	4 (67)	4 (67)
1994[d]	5 (71)	1 (20)	1 (20)
1995[d]	6 (86)	4 (67)	4 (67)
1996[d]	6 (75)	5 (83)	5 (83)
1997[d]	6 (75)	3 (50)	3 (50)
Soutpansberg			
1989[d]	5 (100)	2 (40)	2 (40)
1990[d]	6 (100)	3 (50)	3 (50)
1991	7 (100)	6 (86)	5 (71)
1992	7 (100)	5 (71)	3 (43)
1993	6 (86)	5 (83)	5 (83)
1994[d]	6 (100)	2 (33)	2 (33)
1995[d]	6 (100)	3 (50)	3 (50)
1996[d]	3 (60)	3 (100)	3 (100)
1997[d]	2 (29)	2 (100)	2 (100)
Lanners			
Soutpansberg			
1991	9 (100)	9 (100)	7 (78)
1992	9 (100)	7 (78)	7 (78)
1993	8 (89)	7 (88)	7 (88)

[a] (% of surveyed territories)
[b] pairs which laid at least one egg (% of territorial pairs)
[c] pairs which fledged at least one young (% of territorial pairs)
[d] one-visit surveys

***Appendix 10** Overall breeding performance of Peregrines and Lanners in three areas of South Africa in each year of the study*

population/ year	clutch size (*n*)	brood size[a] (*n*)	mean number of young fledged per		
			successful pair (*n*)	breeding pair (*n*)	territorial pair (*n*)
Peregrines					
Cape Peninsula					
1989	3.00 (1)	2.00 (1)	2.00 (1)	2.00 (1)	0.40 (5)
1990	3.50 (2)	2.67 (3)	2.50 (4)	2.00 (5)	1.11 (9)
1991	2.67 (3)	2.33 (3)	2.50 (2)	1.67 (3)	0.62 (8)
1992	2.25 (4)	2.25 (4)	2.33 (3)	1.40 (5)	0.64 (11)
1993	3.00 (4)	2.00 (4)	2.29 (7)	2.29 (7)	1.33 (12)
1994	2.75 (8)	2.00 (8)	2.11 (9)	1.73 (11)	1.58 (12)
1995	2.67 (9)	1.89 (9)	2.29 (7)	1.33 (12)	1.07 (15)
1996	2.90 (10)[b]	1.36 (11)	1.67 (3)	0.55 (9)	0.31 (16)
1997	2.80 (10)	2.70 (10)	2.47 (15)	2.31 (16)	2.31 (16)
Orange River					
1989[c]	-	-	2.50 (4)	2.50 (4)	2.50 (4)
1990	3.00 (1)	-	2.20 (5)	2.20 (5)	2.20 (5)
1991[c]	-	-	2.20 (5)	2.20 (5)	1.83 (6)
1992[c]	-	-	2.50 (4)	2.50 (4)	2.00 (5)
1993[c]	-	-	2.25 (4)	2.25 (4)	1.50 (6)
1994[c]	-	-	2.00 (1)	2.00 (1)	0.40 (5)
1995[c]	-	-	2.75 (4)	2.75 (4)	1.83 (6)
1996[c]	-	-	2.75 (4)	2.75 (4)	2.20 (5)
1997[c]	-	-	2.50 (2)	2.50 (2)	1.00 (5)
Soutpansberg					
1989[c]	-	-	2.50 (2)	2.50 (2)	1.00 (5)
1990[c]	-	2.50 (2)	2.67 (3)	2.67 (3)	1.33 (6)
1991	3.00 (4)	2.50 (6)	2.60 (5)	2.17 (6)	1.86 (7)
1992	3.00 (4)	3.00 (5)	2.00 (2)	1.00 (4)	0.67 (6)
1993	3.00 (4)	2.60 (5)	2.40 (5)	2.40 (5)	2.00 (6)
1994[c]	4.00 (1)	3.00 (2)	3.00 (1)	3.00 (1)	0.60 (5)
1995[c]	4.00 (1)	3.00 (1)	2.33 (3)	2.33 (3)	1.17 (6)
1996[c]	-	-	2.33 (3)	2.33 (3)	2.33 (3)
1997[c]	-	-	2.00 (1)	2.00 (1)	2.00 (1)
Lanners					
Soutpansberg					
1991	3.33 (6)	2.62 (8)	3.14 (7)	2.44 (9)	2.44 (9)
1992	5.00 (1)	3.40 (5)	2.86 (7)	2.86 (7)	2.22 (9)
1993	3.20 (5)	2.57 (7)	2.57 (7)	2.57 (7)	2.25 (8)

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[a] per breeding pair
[b] including two replacement clutches
[c] maximum figures based on data from one-visit surveys in some or all years

Appendix 11 Average weather conditions in each of three months spanning the pre- and early breeding seasons[a] *of Peregrines and Lanners in three areas of South Africa*

month/ variable	Cape Peninsula[b]	Orange River[b]	Soutpansberg	
			Peregrines[c]	Lanners[d]
Month 1				
mean daily min. temp. (°C)	10.4	8.1	7.2 (6.7)	5.3
mean daily max. temp. (°C)	18.4	25.1	25.0 (24.3)	23.4
rainfall (mm)	68.7	2.2	3.8 (1.4)	6.1
number of rain-days	10.2	1.1	1.1 (0.7)	2.3
Month 2				
mean daily min. temp. (°C)	11.7	12.2	11.5 (12.3)	6.7
mean daily max. temp. (°C)	20.1	29.9	28.2 (28.9)	24.3
rainfall (mm)	50.3	4.0	9.6 (6.1)	1.2
number of rain-days	7.3	0.6	2.0 (1.3)	0.7
Month 3				
mean daily min. temp. (°C)	13.3	14.6	14.6 (15.4)	12.3
mean daily max. temp. (°C)	21.6	32.3	29.1 (30.1)	28.9
rainfall (mm)	33.9	3.3	35.0 (16.2)	6.1
number of rain-days	6.2	1.0	4.4 (3.8)	1.3

[a] months 1, 2 and 3 respectively: Cape Peninsula – September, October, November; Orange River and Soutpansberg Peregrines – August, September, October; Soutpansberg Lanners – July, August, September

[b] averages for the years 1989–1997

[c] averages for the years 1989–1997, with averages for 1991–1993 in parentheses

[d] averages for the years 1991–1993

Appendix 12 *Nest site use, density and breeding performance of Peregrine populations around the world, from recent published studies of pristine or recovered populations*

study area	Mackenzie River, Canada	Colville River, Alaska, U.S.A.	Finland	north and central Greenland
reference	Bromley & Mathews 1988	Ambrose *et al.* 1988	Lindberg *et al.* 1988	Mattox & Seegar 1988
latitude	± 69° N	± 69° N	± 68° N	± 67° N
pair-years	73	157	229	121
inter-pair distance (km)	-	-	-	-
km² per pair	-	-	-	92
mean cliff height (m)	-	-	0	-
minimum cliff height (m)	-	-	0	27
maximum cliff height (m)	-	-	-	120
% occupancy	36	75	-	70
% breeding	-	-	100	-
% successful	79	60	76	82
clutch size	-	-	3.35?	-
young fledged per territorial pair (range)	1.86 (1.2–2.6)	1.63 (1.3–2.0)	1.62 (1.5–2.1)	2.40 (2.3–2.6)
young fledged per successful pair (range)	2.36 (2.2–2.6)	2.73 (2.4–3.3)	2.47 (2.3–2.6)	2.96 (2.6–3.2)

Appendix 12 continued...

study area	upper Yukon River, Alaska, U.S.A.	Norway	Keewatin, Canada	south Greenland
reference	Ambrose *et al.* 1988	Lindberg *et al.* 1988	Court *et al.* 1988	Falk & Møller 1988
latitude	± 65° N	± 65° N	± 62° N	± 61° N
pair-years	135	134	101	58
inter-pair distance (km)	-	-	3.3	-
km^2 per pair	-	-	17	240
mean cliff height (m)	-	-	± 20	-
minimum cliff height (m)	-	-	7	-
maximum cliff height (m)	-	-	30	-
% occupancy	87	-	-	70
% breeding	-	72	90	-
% successful	84	60	73	56
clutch size	-	-	3.64	-
young fledged per territorial pair (range)	2.15 (1.6–3.0)	1.22 (0.9–1.8)	2.03 (1.8–2.4)	1.76 (1.5–1.9)
young fledged per successful pair (range)	2.67 (2.3–3.2)	2.03 (1.7–2.2)	2.76 (2.4–3.1)	2.72 (2.5–3.2)

Appendix 12 continued...

study area	Ungava Bay, Canada	northern & western Highlands, Scotland	central Highlands, Scotland	southern Highlands, Scotland
reference	Bird & Weaver 1988	Ratcliffe 1993	Ratcliffe 1993	Ratcliffe 1993
latitude	± 59° N	± 58° N	± 57° N	± 56° N
pair-years	54	137	227	392
inter-pair distance (km)	-	-	-	5.4?
km² per pair	-	-	-	-
mean cliff height (m)	-	± 40	± 45	± 35
minimum cliff height (m)	-	<20	<20	<20
maximum cliff height (m)	-	>90	>90	>90
% occupancy	66	-	-	-
% breeding	-	63	77	71
% successful	94	49	57	58
clutch size	-	3.46	-	-
young fledged per territorial pair (range)	2.56 (2.3–2.9)	0.98	1.35	1.23
young fledged per successful pair (range)	2.69 (2.4–3.2)	2.08? (1.7–2.2)	2.15	2.15

study area	southern Scotland	northern England	Northern Ireland	Langara Island, Canada
reference	Ratcliffe 1993	Ratcliffe 1993	Crick & Ratcliffe 1995	Nelson 1990
latitude	± 55° N	± 54° N	± 54° N	± 54° N
pair-years	525	622	72	61
inter-pair distance (km)	± 4.2	± 4.0	-	-
km^2 per pair	-	-	-	-
mean cliff height (m)	± 20	-	-	-
minimum cliff height (m)	<11	-	-	-
maximum cliff height (m)	>90	-	-	-
% occupancy	-	-	-	-
% breeding	80	83	-	-
% successful	49	55	63	65
clutch size	3.42	3.45	3.24	-
young fledged per territorial pair (range)	1.09	1.41	1.42	-
young fledged per successful pair (range)	2.27	2.43	2.41	2.24

Appendix 12 continued...

study area	Wales	southwestern England	western Alps, Italy	northern Apenines, Italy
reference	Ratcliffe 1993	Ratcliffe 1993	Fasce & Fasce 1988	Fasce & Fasce 1988
latitude	± 53° N	± 51° N	± 45° N	± 44° N
pair-years	262	197	79	60
inter-pair distance (km)	± 4.5	± 4.1	11.6	-
km² per pair	-	-	-	-
mean cliff height (m)	± 35	-	-	-
minimum cliff height (m)	<11	-	-	-
maximum cliff height (m)	>90	-	-	-
% occupancy	-	-	-	-
% breeding	77	84	-	-
% successful	59	65	68	57
clutch size	3.40	-	-	-
young fledged per territorial pair (range)	1.22	1.51	1.99 (0.5–2.4)	1.20 (0.5–1.8)
young fledged per successful pair (range)	2.05	2.29	2.50 (1.0–2.8)	2.10 (1.6–2.8)

study area	Spain	Rocky Mountains, U.S.A.	northwest Arizona, U.S.A.	southeast Arizona, U.S.A.
reference	Heredia *et al.* 1988	Enderson *et al.* 1988	Ellis 1988	Ellis 1988
latitude	± 40° N	± 36° N	± 36° N	± 32° N
pair-years	262	93	58	64
inter-pair distance (km)	-	-	-	-
km^2 per pair	-	-	-	-
mean cliff height (m)	-	-	-	-
minimum cliff height (m)	-	-	-	-
maximum cliff height (m)	-	-	-	-
% occupancy	-	-	92	63
% breeding	-	-	-	-
% successful	-	-	87	58
clutch size	-	-	-	-
young fledged per territorial pair (range)	1.73	1.73 (0.0–3.0)	-	-
young fledged per successful pair (range)	-	2.14 (0.0–3.0)	1.74	1.36

study area	Texas/New Mexico, U.S.A.	Baja California, Mexico	Sierra Madre, Mexico	Peru & Ecuador
reference	Hunt *et al.* 1988	Porter *et al.* 1988	Hunt *et al.* 1988	McNutt *et al.* 1988
latitude	± 32° N	± 28° N	± 26° N	± 10° S
pair-years	81	101	46	13
inter-pair distance (km)	-	-	-	-
km^2 per pair	-	-	-	-
mean cliff height (m)	-	-	-	115?
minimum cliff height (m)	-	-	-	100
maximum cliff height (m)	-	-	-	120
% occupancy	87	84	-	-
% breeding	-	-	-	-
% successful	37	-	64	63
clutch size	-	-	-	-
young fledged per territorial pair (range)	1.01 (0.3–2.2)	1.08 (0.9–1.5)	1.25 (0.7–1.7)	1.44 (0.67–3.0)
young fledged per successful pair (range)	1.99 (1.0–3.0)	2.14 (1.6–2.8)	1.95 (1.7–2.5)	1.50 (1.0–3.0)

Appendix 12 continued...

study area	Zimbabwe	Waterberg, Namibia	Soutpansberg, South Africa	Orange River, South Africa
reference	Hartley *et al.* 1995	Brown & Cooper 1987	this study	this study
latitude	± 18° S	± 20° S	± 23° S	± 28° S
pair-years	29?	-	48	49
inter-pair distance (km)	-	5.1	9.7	6.3
km² per pair	-	-	-	-
mean cliff height (m)	-	85	114	82
minimum cliff height (m)	-	50	75	25
maximum cliff height (m)	-	140	180	140
% occupancy	-	-	86	85
% breeding	-	-	65	71
% successful	-	-	58	71
clutch size	-	-	3.14	-
young fledged per territorial pair (range)	1.45	-	1.36 (0.7–2.3)	1.70 (0.4–2.5)
young fledged per successful pair (range)	1.83	-	2.44 (2.0–3.0)	2.42 (2.0–2.8)

Appendix 12 continued...

study area	central & northern Argentina	Cape Peninsula, South Africa	Nuriootpa, South Australia	Canberra, Australia
reference	McNutt *et al.* 1988	this study	Olsen & Olsen 1988b	Olsen & Olsen 1988a/1989a & b
latitude	± 30° S	± 34° S	± 36° S	± 36° S
pair-years	33	106	64?	>300
inter-pair distance (km)	-	5.6	4.7?	4.3
km^2 per pair	-	-	-	150
mean cliff height (m)	-	79	-	25
minimum cliff height (m)	-	20	20	10
maximum cliff height (m)	-	280	84	60
% occupancy	-	96	91	86
% breeding	-	68	88	75
% successful	97	49	-	58
clutch size	-	2.78	-	-
young fledged per territorial pair (range)	2.72 (2.0–4.0)	1.11 (0.3–2.3)	2.00 (1.6–2.2)	1.44 (1.2–1.8)
young fledged per successful pair (range)	2.75 (2.2–4.0)	2.29 (1.7–2.5)	2.20 (1.8–2.2)	2.16 (1.9–2.6)

Appendix 12 continued...

study area	Victoria, Australia	Tasmania, Australia	southern Chile & Argentina
reference	Pruett-Jones *et al.* 1981	Olsen & Olsen 1988b	McNutt *et al.* 1988
latitude	± 37° S	± 42° S	± 48° S
pair-years	77	320?	80
inter-pair distance (km)	-	13.8?	-
km^2 per pair	-	-	-
mean cliff height (m)	29	49	-
minimum cliff height (m)	4	7	-
maximum cliff height (m)	75	200	-
% occupancy	-	68	-
% breeding	84	75	-
% successful	60	-	75
clutch size	2.81	-	-
young fledged per territorial pair (range)	1.21	1.9 (1.3–2.3)	1.79 (1.3–3.0)
young fledged per successful pair (range)	2.00	2.5 (2.2–3.0)	2.47 (1.7–3.0)