

Ecology of Taita *Falco fasciinucha*, Peregrine *F. peregrinus minor* and Lanner *F. biarmicus* Falcons in Zimbabwe

R.R. Hartley

ABSTRACT

All Taita *Falco fasciinucha* and most African Peregrine *F. peregrinus minor* Falcons were found breeding along escarpments, gorges and inselbergs in well-wooded country, mainly along river systems in the Zambezi Valley (80% Taitas, N = 16; 37% of Peregrines, N = 50), where Peregrines outnumbered Taitas 3:1 and Lanner Falcons *F. biarmicus* 10:1. Most Lanner nests (67%, N = 155) were found in open or woodland habitats in domed inselberg and kopje terrain, where they outnumbered Peregrines 3:1 and where Taitas were rarely seen. Peregrines and Lanners competed with Taitas for breeding sites and for prey, and consequently Taitas were relatively absent from areas which also hosted the other two species. While cliffs >100 m were favoured by Taitas (38%, N = 7) and Peregrines (23%, N = 28), cliffs <25 m (25%, N = 5) and 30-35 m (31%, N = 34) were used by them respectively. All Taita and Peregrine nests were on cliffs, where cavities (Taitas 73%, N = 19; Peregrines 46%, N = 51) and sheltered ledges were used mainly. Most Lanner nests (88%, N = 203) were on cliffs (ledges 63%, N = 110; cavities 21%, N = 38) and 50% (N = 56) were on features <25 m high. Lanners also used stick nests (32%, N = 72) on cliffs (22%, N = 45), in trees (96%, N = 27) and on pylons (100%, N = 2), while Lanners (16%, N = 36) and Peregrines (8%, N = 11) also bred in quarries and on buildings.

The main prey of Taitas was small to medium sized birds (mean = 40,9 g) from woodland (64%) and cliff (32%) habitats, of Peregrines was medium sized birds (mean = 139,7 g), especially doves (39%) from woodland (84%), and of Lanners was medium sized birds (mean = 188 g) from woodland (49%) and human (45%) habitats, where key prey was feral pigeons *Columba livia* and poultry. The rarity of the Taita is probably determined by its more specialised habitat requirements and possibly also by its interspecific relationship with the Peregrine, while the population of the generalist Lanner may be expanding with land clearance in Zimbabwe.

INTRODUCTION

Taita *Falco fasciinucha*, African Peregrine *F. peregrinus minor* and Lanner *F. biarmicus* Falcons are resident in Zimbabwe (hereafter Taita, Peregrine and Lanner respectively). The much rarer Siberian Peregrine *F. peregrinus calidus* is a non-breeding Palaearctic migrant which has rarely been

encountered in Zimbabwe (Irwin 1981; Hartley 1998). Throughout its range in Africa, the Taita is sympatric with the much larger Peregrine (Hunter *et al.* 1979; Thomsett 1988; Moller 1989; Jenkins 1991; Hartley *et al.* 1993) and the two species may compete for nest sites and prey (Thomson 1984; Hustler 1989; Hartley *et al.* 1993). Throughout their shared range, the Peregrine is apparently dominant and it possibly affects the distribution and abundance of the much rarer Taita (Thomson 1984; Hustler 1989; Hartley *et al.* 1993). In Zimbabwe, it is possible that there are more than 60 pairs of Taitas (Hartley 1995) and 350-400 pairs of Peregrines (Hartley 1993a).

The Peregrine is a little studied, uncommon breeding resident in Africa south of the Sahara (Brown *et al.* 1982; Cade 1982; Steyn 1982), although it appears to be more common in Zimbabwe (Irwin 1981; Thomson 1984; Hartley 1992; Harrison *et al.* 1997), Kenya (Thomsett 1988) and in the Western Cape Province of South Africa (Pepler & Martin 1988; Jenkins 1994). Despite being a specialist hunter of birds (Ratcliffe 1980; Cade 1982), the Peregrine has proved highly adaptable over its cosmopolitan range (Cade *et al.* 1988), and in Africa it is resident over a wide range of habitats, including deserts (Braby *et al.* 1987). However, in Africa it appears to be best represented in tropical woodlands (Hustler 1983; Tarboton & Allan 1984; Thomson 1984; Hartley 1992) and fynbos (Jenkins 1994). Many of the investigations on the Peregrine in Africa have focussed on its apparent rarity, with suggested reasons being: a) its dependence on cliffs in woodland habitats; b) the role of water and related patchiness of food resources; c) the influence of cliff height, latitude and pesticides; and d) competition with the sympatric Lanner (Thomson 1984; Mendelsohn 1988; Jenkins 1991, 1992a & b, 1994; Hartley 1992). Both Lanners and Peregrines occur throughout Zimbabwe (Irwin 1981; Harrison *et al.* 1997). Lanners breed on a wide range of cliffs and also in old stick nests in trees and on pylons (Thomson 1984). Lanners are more common in more open habitats and it has been estimated that there are over 1000 pairs in Zimbabwe (Thomson 1984).

Based on subjective observations, Thomson (1984) suggested that: 1) the rarity of the Taita is determined by its interspecific relationship with the Peregrine; 2) the site requirements and breeding season of Peregrines and Lanners are the principal factors determining their respective population status in Zimbabwe; and 3) the Lanner is an open country species whose range has probably increased with recent deforestation in Africa. This study investigates these hypotheses and presents sightings and specimen data on distribution, abundance, nest site characteristics, morphology, hunting, prey, habitat requirements and habitat changes, based on 20, 136, and 231 pairs of Taitas, Peregrines and Lanners respectively.

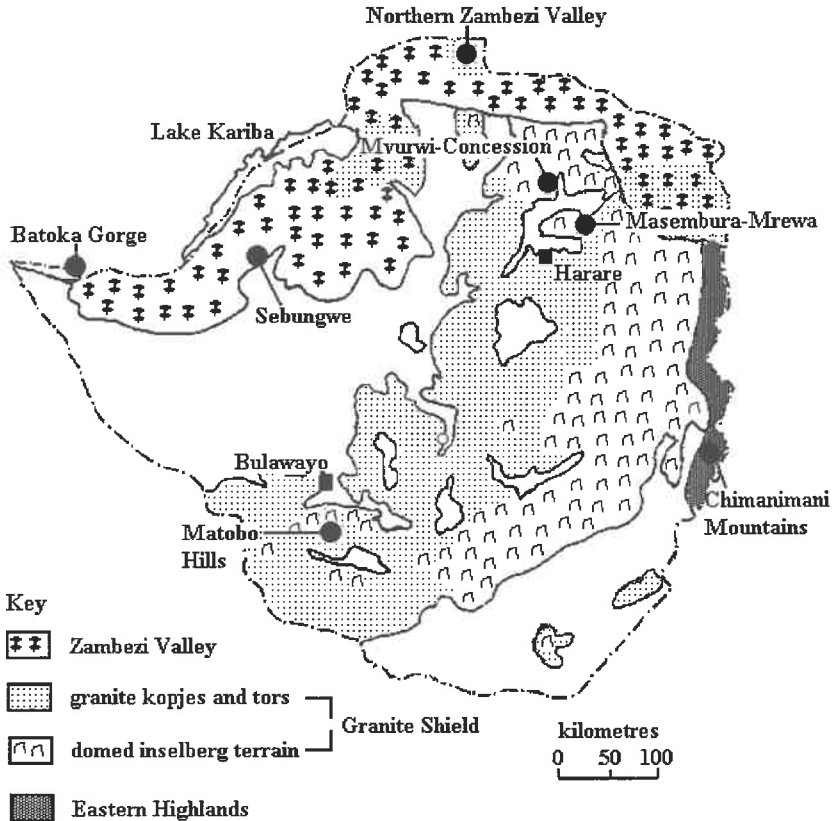
STUDY AREA

Zimbabwe covers an area of 390,460 km² (Zinyama & Whitlow 1986) within the Afro-tropical region. The physical background has been described by Irwin (1981). There are four main geographical regions: the lowveld (<600 m elevation), middleveld (600-1000 m), highveld (>1000 m) and montane. Generally, temperature, rainfall and vegetation type are coincident with these altitudinal zones. Annual rainfall is mainly from November to March, with a national mean of 647 mm (range of 335-1193 mm), but varying from 147-2640 mm in different parts of the country in different years (Department of Meteorological Services *in litt.*). Although the principal vegetation type is *Brachystegia* (Miombo) woodland, 24 sub-types have been described by Wild (1965).

Key woodland habitats are mopane *Colophospermum mopane* in the drier (400-712 mm annual rainfall) lowveld and middleveld areas (zone 1 - Zambezi Valley; Fig. 1); varying combinations of *Julbernardia* and *Brachystegia* in the wetter (700-1500 mm) middleveld (zone 1) and highveld areas (zone 2 - Mvurwi-Mrewa), and *Terminalia* in granitic terrain of the middleveld (700-800 mm; zone 3 - Matobo Hills).

Topographical features used for nesting by these falcons include tors, kopjes, domed inselbergs, mesas, mountain cliffs, escarpments, river cliffs and gorges (Lister 1993; Table 1). Tors are relatively small piles of granite boulders extending 5-40 m above the general topography. Kopjes are small granite hills up to 70 m high, comprising large rectangular boulders interspersed with small patches

Figure1. Principal falcon breeding zones in Zimbabwe



of soil and vegetation. Domed inselbergs, also called bornhardts, are large granite features which usually range from 100-500 m above the general topography and vary from almost symmetrical whalebacks to irregular sugar-loaf features. Kopjes, and sometimes tors, are found among domed inselbergs, but are also frequent over the remainder of the granite shield. All such cliff habitats are abundant over wide areas of the country, of which about 30% is covered by granitic domed inselbergs (Fig. 1; Whitlow 1980a), while mountain ranges, and escarpments and gorges, characterise the eastern border and the main river systems (especially the Zambezi and Save) respectively.

The quality and abundance of natural habitats is related to three land-use categories. State Land (National Parks Estate = 12,7%; Forestry Areas = 2,3% of Zimbabwe) comprises protected areas with natural densities of breeding raptors. General Land (32% of the country) is privately owned, has a mean density of 7,6 persons/km², comprises mainly ranchlands with natural habitats still intact and relatively undamaged (Whitlow 1988; Hartley *et al.* 1996), and in many areas has densities of breeding raptors that compare favourably with protected areas. On Communal Lands (42% of the country, but 60% of the human population at a mean density of 25,5 persons/km², Zinyama & Whitlow 1986), habitat quality has declined rapidly and 60% of the area is either overpopulated or grossly overpopulated (Whitlow 1988), mainly with peasant farmers. Deforestation in several of these areas has reached 10% per year (Whitlow 1980b), especially in areas with domed inselberg terrain which comprise 64% of Communal Lands (Whitlow 1980a, 1988).

Table 1. Topographical and other features used for nesting by Taita, Peregrine and Lanner Falcons in Zimbabwe.

% Feature used	Species		
	Taita (n = 20)	Peregrine (n = 136)	Lanner (n = 231)
Tor			7.4
Kopje		1.5	26.0
Domed Inselberg (Bornhardt)		36.8	33.7
Mesa	20.0	9.5	0.9
Mountain cliff/Escarpment	5.0	12.5	2.2
River cliff		12.5	
Gorge	75.0	19.1	1.3
Quarry		4.4	13.8
Building		3.7	1.7
Pylon			0.9
Tree			12.1

METHODS

Surveys were conducted during the breeding season by members of the Zimbabwe Falconers' Club (ZFC; Hartley 1993b). Work on Taitas and Peregrines sometimes involved The Peregrine Fund Inc. (TPF) and was part of a formal programme between the ZFC and the Department of National Parks and Wild Life Management (DNPWLM; Hartley 1993b). Data were collected on habitat, nest type, cliff height, position and aspect. Nest record cards from the Natural History Museum of Zimbabwe were also used, and mainly involved Lanners (n = 58).

Three contrasting zones surveyed between 1990 and 1994 were assessed for ecological contrasts favoured by Taitas, Peregrines and Lanners. Zone 1 included three study areas in the Zambezi Valley (Fig. 1). Zone 2 included an arc of granite dwala and kopje terrain stretching from privately-owned, relatively undisturbed habitats on General Land around Mvurwi-Concession, to tribal-owned, significantly deforested Communal Lands around Masembura-Domboshava-Mrewa. Zone 3 was the mainly kopje terrain of the Matobo Hills (Gargett 1990), including National Parks Estate (protected), General and Communal Lands. For each nest site in each of these areas, a quality index (QI) was calculated that included three key components (each with a score of 0-2, maximum possible score 6, after Manzi & Perna 1994): 1) maximum height of cliff, <35m = 0; 36-100 m = 1; >100 m = 2; 2) complexity of site, single cliff = 0; group of cliffs with one aspect = 1; group of cliffs with more than one aspect = 2; 3) dominance, the angle of view with no intervening obstacles for at least 1 km, <30° = 0, 30°-90° = 1 and >90° = 2.

Table 2. Taita, Peregrine and Lanner Falcon nest sites in Zimbabwe, according to land use category.

Species (n)	% Land use category		
	N.Park/state land	General land	Communal land
Taita (n = 20) ¹	84.2		15.8
Peregrine (n = 136)	35.6	28.1	36.3
Lanner (n = 231)	10.6	56.4	32.9

¹ includes two sites on Zambian side of Batoka Gorge, Zambezi

Prey data for Taitas were sourced from Hartley *et al.* (1993) and my unpublished notes, for Peregrines from Hustler (1983), Hallamore (1972) and my unpublished notes, and for Lanners from

the unpublished notes of myself, G.Hall and W.R. Thomson. Prey were identified from pluckings, remains, pellets and from observations at all sites, during and outside of the breeding season. Identification was based on comparisons with reference material held by the Natural History Museum of Zimbabwe and with my own catalogue of avian prey (126 species). It is likely that reptiles and mammals were under-represented for the generalist Lanner (Simmons *et al.* 1991). Captive Taitas (N = 16) and Peregrines (N = 22), and wild-caught Lanners (N = 29), were weighed to the nearest gram on an Ohaus triple-beam balance, and some were also measured (following Biggs *et al.* 1978 and Mendelsohn *et al.* 1989). Nomenclature follows Maclean (1993).

The laying date of the first egg was estimated by backdating from the estimated age of the chick(s) in each nest. It was assumed that eggs were laid at 3-day intervals and that incubation and fledging took 32 days (but 34 days for Taita, W. Heck & RRH pers. obs.) and 42 days respectively.

RESULTS

1. Status and distribution

1.1. National

The Peregrine and Lanner occurred throughout the country, while the Taita was more restricted. Of 27 Peregrines recovered or trapped since 1965, only three were *F. p. calidus* (Hartley 1998). Only two Taitas were recovered over this period. All Taitas and most Peregrines were found breeding in well wooded country along escarpments, gorges and inselbergs (Table 1), mainly along river systems in the Zambezi Valley (16/20 Taita nests; 50/136 Peregrine nests) where Lanners were less common. Taitas and Peregrines were found breeding at altitudes of 350-2200 m a.s.l. Taitas and Peregrines were also found along the montane eastern highlands, including in dry deciduous woodland and in the mountain heathlands overlooking moist miombo woodlands. Lanners were found mainly (N = 155) in open and woodland habitats on the granite shield, where they were more frequent than Peregrines and where Taitas were rarely seen.

Peregrines predominated in undisturbed woodland habitat with isolated vertical rock formations overlooking river systems or springs. The most extreme examples of this phenomenon were: 1) along a line of 30 m high sandstone cliffs in the Save valley where three pairs of Peregrines bred at a mean internest distance of 1,4 km, and 2) on a massive sandstone mesa in the Zambezi valley where two pairs occupied back-to-back cliffs only 0,35km apart. Where there are multiple vertical rock formations offering a wide choice of cliffs, such as in long convoluted gorge systems, Taitas may co-exist as a breeding population with Peregrines. This is also true of the mountainous Chimanimani area which has at least three pairs of Taitas and six pairs of Peregrines. By contrast, Taitas were rarely encountered in areas that had been significantly altered by humans.

Of 20 different Taita sites checked from 1990-97, 15 were occupied and five were abandoned. Of 99 different Peregrines sites checked from 1990-97, 73 were occupied, seven were abandoned and 19 were replaced by Lanners, eight of these on domed inselbergs in deforested Communal Lands (Table 1). Most Taita sites and 63.7% of Peregrine sites occurred either in protected areas or on relatively undisturbed habitats on General Land (Table 2). On Communal Lands, Lanners appear to have benefited from land clearing, while Taitas and Peregrines have not.

1.2. Domed inselberg and kopje terrain

Peregrines and Lanners competed mainly for large domed inselbergs in woodlands (Fig. 1, Table 1), and nine of these features were shared by both species: in each case the falcons occupied cliffs within 0,5 km (but out of sight) of each other. Of 23 Peregrine sites occupied by Lanners, 14 were on large domed inselbergs. Of five Lanner sites occupied by Peregrines, four were on large domed inselbergs, two in well wooded General Land, and two in deforested Communal Lands. In relatively undisturbed habitats in domed inselberg terrain (Mvurwi-Concession - zone 2; Fig. 1) six pairs of Peregrines were matched by Lanners 1:1.2. Mean internest distances for Peregrines and Lanners were 24.6 km (SD = 7.64 km) and 16.2 km (SD = 16.09 km) respectively. In the deforested areas of

the Communal Lands nearby (Masembura-Dombashawa-Mrewa) five pairs Peregrines were outnumbered by Lanners 1:3.3 and mean internest distances were 23.9 km (SD = 13.56 km) and 6.1 km (SD 2.62 km) respectively. Most of the deforestation was on the flat, undulating pediments, while the scree slopes remained wooded. By contrast, in the kopje terrain of the Mangwende Communal Land south of Mrewa there were no Peregrines, while the mean inter-nest distance for six pairs of Lanners was 4.8 km (SD = 0.4 km).

Throughout the granite shield tors and kopjes (33%) were used by Lanners (Table 1) and only two large kopjes were used by Peregrines: one an alternate site, and the other, a nest on a vertical granite finger, was occupied only once. As a general rule, Peregrines did not breed on tors and kopjes. This trend is further supported by the pattern in the Matobo Hills (zone 3), which consists primarily of kopjes. Here 2-3 pairs of Peregrines (mean inter-nest distance = 10.2 km, SD = 3.3 km) also bred mainly on large domed inselbergs, leaving Lanners (n = 21; mean inter-nest distance = 6.9 km, SD 3.62 km) to dominate the tors, kopjes and remaining domed inselbergs, many of which are occupied by Black Eagles. Lanners (13%) frequently use old, and sometimes even new nests of Black Eagles *Aquila verreauxii*. Peregrines and also Taitas rarely use old stick nests for breeding (Table 3). Although Taitas were seldom encountered in granite terrain and have not yet been recorded breeding in such habitats in Zimbabwe, it is likely that they do so as a Taita was seen at very close range near Centenary in 1995 (J. Hough *in litt.*).

1.3. Zambezi Valley

In the Zambezi Valley, Peregrines (N = 50) outnumbered Lanners (N = 5), and also outnumbered Taitas 3:1. In the Sebungwe area of the Zambezi Valley, two Lanner sites occurred on mesas, shared with pairs of Peregrines 1.1 km and 2.2 km away respectively. The latter zone once hosted a pair of Taitas which nested on a low cliff which faced an occupied Peregrine site 3.9 km away. However, since a pair of Lanners took over the Peregrine site, the Taitas have left and have not been relocated, while the Peregrines have bred elsewhere on the same feature. In a more rugged area nearby, a deep gorge once hosted two pairs of Taitas and two pairs of Peregrines, but they were then joined by a pair of Lanners. The Taitas originally nested 1.9 km apart, but only 0.7 km and 1.1 km from where the Lanners nested. Since the arrival of the Lanners, only one pair of Taitas has been seen, but the nearest Peregrines, 1.7 km and 3 km away respectively, were still there. Twelve pairs of Peregrines and four pairs of Taitas have been found in this rugged gorge (Peregrines = 6; Taitas = 4) and escarpment (Peregrines = 6) terrain. Mean internest distance for Peregrines was 4.96 km (SD = 2.59 km). Over the past 30 years, elephants *Loxodonta africana* have caused extensive damage to some of the woodlands in this zone, which may have favoured the Lanner. In another area of the northern Zambezi Valley, three pairs of Taitas and three pairs of Peregrines were found on isolated mesas in dry deciduous woodland. The two closest Taita sites were 5.4 km apart, while the internest distance for Peregrines was 6.3 km (SD = 2.7 km).

The highest recorded density of falcons was in the Batoka Gorge system below Victoria Falls, where 13 pairs of Peregrines and six pairs of Taitas were found. The mean inter-nest distances for Taitas and Peregrines were 4.62 km (SD = 2.38 km) and 3.49 km (SD = 2.0 km) respectively, or one pair of falcons of either species every 3.84 km. This is probably an underestimate, as it is likely that there were 8-10 pairs of Taitas and 15-18 pairs of Peregrines along this section (Hartley 1993a). As for the Sebungwe area, the extensive system of convoluted cliffs has provided many opportunities for nesting and has probably led to the significant concentration of Taitas.

1.4. Human altered environments

Both Lanners and Peregrines have adjusted to human altered environments. Both species bred in quarries (Table 1) and on dam walls. In the quarries of the Shurugwi area, up to six pairs of Lanners and two pairs of Peregrines have bred at mean internest distances of 2.6 km (SD = 1.71 km) and 12.8 km respectively. Similar clusters of Lanners occurred in the quarries of Mashava (six pairs) and Zvishavane (seven pairs).

Up to two pairs of Peregrines and a pair of Lanners have bred in Harare city. A pair of Peregrines

has attempted breeding in Bulawayo city, while both species can be frequently encountered in either centre. Five and 14 Peregrines have been recovered/trapped in and around Bulawayo and Harare cities respectively. Over seven days, in agricultural lands on the edge of Harare, one Peregrine and five Lanners were trapped and ringed. These falcons were all attracted to maize and soya bean lands which hosted large numbers of doves (*Streptopelia semitorquata*, *S. capicola* and *S. senegalensis*) and Redbilled Queleas *Quelea quelea*. These grain fields have acted as 'funnels' (Hartley 1998) for falcons - tens of thousands of Redbilled Queleas usually occurred in early to mid-winter - that draw in mainly juvenile and immature Lanners. As many as seven Lanners have been seen in the air at once, while others were perched nearby either on the ground or in eucalyptus trees (Hartley 1998).

2. Nest site characteristics and breeding

2.1. Cliff height and quality index

Taitas and Peregrines mainly occupied dominant vertical cliffs, while Lanners occupied these and smaller features, as well as trees (Table 1; Fig. 2). Taitas also bred on very small vertical cliffs (25% <25 m), while Peregrines bred frequently on vertical cliffs with a modest height (30-35 m), but only in the mid- to low altitude woodlands of the Zambezi and Save catchments where they were able to outcompete Lanners. Although Peregrine nests are usually inaccessible, one could walk on to three of these sites despite their being in areas frequented by baboons *Papio ursinus*. In domed inselberg terrain, where there was probably competition with the Lanner, and in the eastern highlands, only large features and mountain cliffs (nearly all >71 m) were used. The most consistently occupied Peregrine nests in domed inselberg terrain were those on cliffs >100 m. Furthermore most cliffs used by Taitas and Peregrines had a commanding height above the valley or plains below (Taitas: range = 30-984 m, mean = 170 m; Peregrines range = 40-1020 m; mean = 251 m) and there is no significant difference between on small (<70 m) and large cliffs (>71 m, $\chi^2 = 2.563$, $P = >0.1$). Half (50.3%) the cliffs used by Lanners were <25 m, and the difference between cliff heights used by Lanners and Peregrines was significant ($\chi^2 = 18.55$, $P = <0.001$).

Mean QIs for all sites tested in the three sample zones were Taitas 2.56 (n = 16); Peregrines 3.92 (n = 56) and Lanners 2.97 (n = 58). Mean cliff heights were 103.5 m (range 20-350 m), 84.4 m (range 24-300 m) and 45.1 m (6-180 m) respectively. In Batoka Gorge, the QI was 4 for Peregrines and 3.8 for Taitas, the limited difference probably relating most to the relative homogeneity of the system. In the Sebungwe area, the QI was 4.19 for Peregrines and 2.8 for Taitas. In the northern Zambezi Valley, the QI was 3 for Peregrines and 0.8 for Taitas, the latter clearly occupying marginal sites. Wherever Taitas occurred, they had to fit in where possible (Hartley *et al.* 1993) and four Taita sites were located near occupied Black Eagle nests, with none of the Peregrine sites so positioned. Both Taitas and Peregrines vigorously defended their nests when eagles passed by (Hartley *et al.* 1993).

2.2. Cavities, ledges and stick nests

Taitas nested in cavities and sheltered ledges, in common with Peregrines (Table 3) and the difference in frequency of use was not significant ($\chi^2 = 4.83$, $P = >0.02$). Cavities provide shade and more easily allow brooding falcons and their young to escape detection from predators. Taitas are especially secretive around the nest (Hartley *et al.* 1993). Furthermore they are able to use much smaller cavities (mean = 0.76 m wide x 0.5 m high x 0.7 m deep m; N = 4) than Peregrines (mean = 2.14 m wide x 1.2 m high x 1.5 m deep; N = 21).

Most Lanner nests were on cliffs (87%; Table 1) where ledges were used mainly, many of these open, and some cavities (Table 3). The difference in frequency of use of these nest types was significant between Lanners and Peregrines ($\chi^2 = 16.57$, $P = <0.001$). Lanners also used old stick nests in trees, pylons, and on cliffs (Table 3). Lanners (15.6%) and Peregrines (8.1%) also bred in quarries and on buildings. Quarry sites used by Peregrines were deep vertical sink holes, not the large open faces used by Lanners.

Figure 2. Cliff height selection for Taita, Peregrine and Lanner Falcons in Zimbabwe.

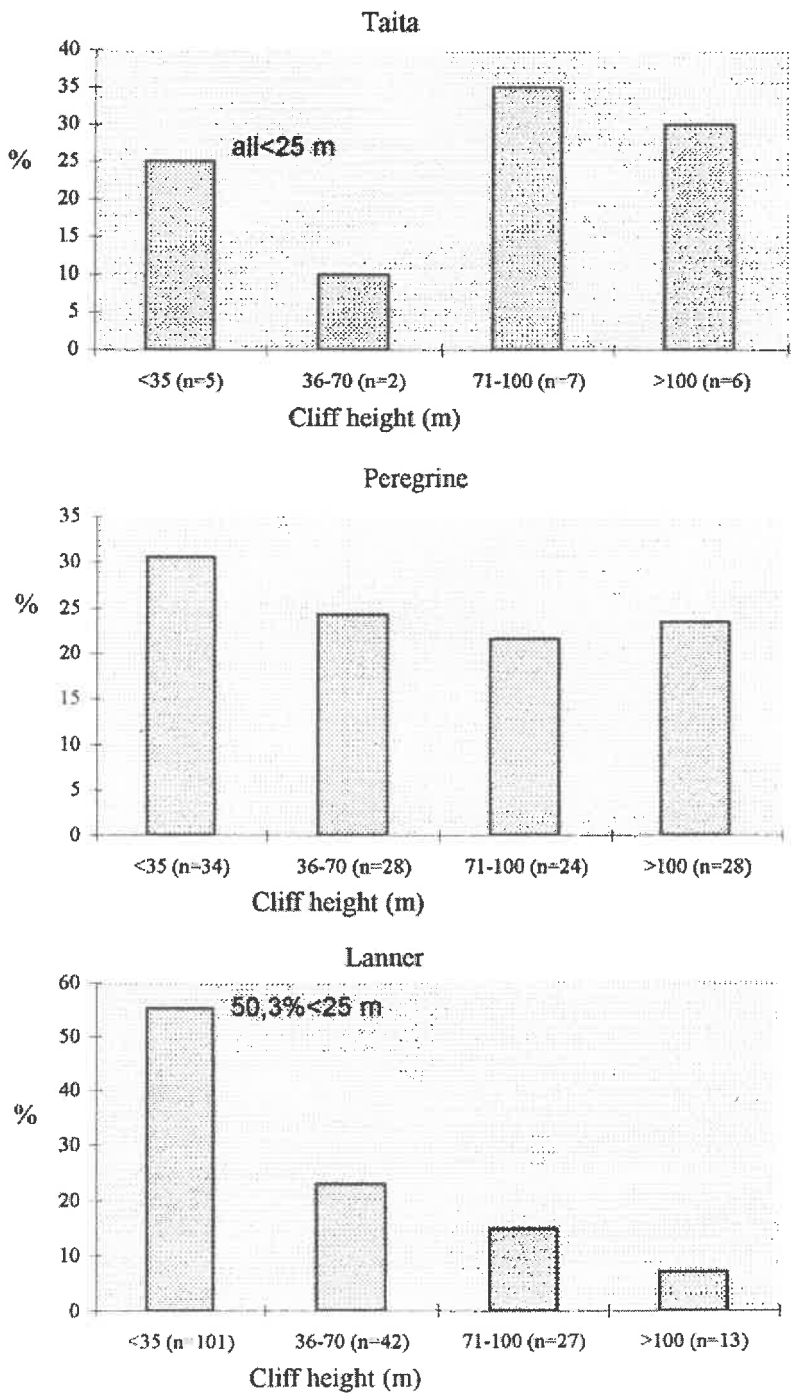


Table 3. Preferred nest sites for Taita, Peregrine and Lanner Falcons in Zimbabwe. Parentheses indicate % old stick nests in ledges, cavities and trees.

<i>Species</i>	<i>Ledge</i>	%Nest sites	
		<i>Cavity</i>	<i>Tree</i>
Taita (n = 26) ¹	26.9 (3.8)	73.1 (3.8)	
Peregrine (n = 104)	51 (2.9)	49 (2)	
Lanner (n = 183)	63.9 (16.4)	20.8 (5.5)	15.3 (96.4) ²

¹ ledges and cavities were used alternately at three sites

² one nest in crotch of tree

By contrast Lanners often took over eagle nests (N = 51), especially Black Eagle (N = 23). Furthermore, there were ten records of Lanners harassing eagles and/or their chicks before they used the eagle nests. There were also suggestions that the Lanners either evicted or killed eagle chicks (N = 3) to achieve their objective. Bateleur *Terathopius ecaudatus* nests were used on eight occasions. Other eagle nests used included Martial *Polemaetus bellicosus*, African Hawk *Hieraaetus spilogaster* and Tawny Eagles *A. rapax*. Other stick nests used included Whitenecked Raven *Corvus albicollis* (N = 15) and Black Stork *Ciconia nigra* (N = 8). Aggressive encounters occurred with Whitenecked Raven (a clutch of Lanner eggs was found broken amongst raven and Lanner feathers) and Lanners also harassed Black Storks.

All three falcon species have been seen dust bathing, but only Taita and Peregrines have been seen water bathing (in small pools). In captivity, Taitas and Peregrines water bath regularly, but Lanners rarely do so. All Taita and Peregrine sites were close to permanent water (Hartley *et al.* 1993). Although a wide range of aspects was chosen by all species, southerly aspects appear to be favoured by Taitas and Peregrines while Lanners favoured east and west aspects (Table 4).

Table 4. % of aspects for nests of Taita, Peregrine and Lanner Falcons in Zimbabwe.

<i>Facing</i>	<i>Species</i>		
	<i>Taita (n = 17)</i>	<i>Peregrine (n = 113)</i>	<i>Lanner (n = 177)</i>
N	5.9	7.1	10.7
NNE	5.9	2.7	1.1
NE	5.9	7.1	11.9
ENE		1.7	
E	11.7	6.2	19.2
ESE		1.7	0.6
SE	5.9	8.0	7.3
SSE	11.7	7.1	0.6
S		13.3	13.0
SSW	11.7	11.5	0.6
SW	17.6	5.3	9.0
WSW		7.1	0.6
W	5.9	4.4	18.1
WNW	5.9	2.6	
NW	5.9	7.1	7.3
NNW	5.9	7.1	

2.3. Laying dates and clutch sizes

Although few observations were conducted outside of the breeding season, some Peregrines have been found at their breeding cliffs in April, at the same early stage as Lanners. However, peak laying periods for Lanners, Peregrines and Taitas were in this order and about a month apart (Table 5). Both Lanner and Peregrine young fledged by the end of September and early November

respectively, near the onset of the rains. At this time there is a sharp influx of prey from three sources a) migratory birds, b) fledglings of resident passerines especially from mid-November onwardss and mainly insectivores (Vernon 1978; Irwin 1981) and c) insects, including termite alates. Insect abundance is often coincident with the onset of the rains in late-October/early November, when juvenile Lanners are becoming independent.

Table 5. Laying dates for Taita, Peregrine and Lanner Falcons in Zimbabwe.

Species	Number per month (%)					
	May	June	July	Aug	Sept	Oct
Taita (n = 21)				9.5	85.7	4.8
Peregrine (n = 81)			3.7	88.9	7.4	
Lanner (n = 112)	0.9	5.4	58.0	33.9	0.9	

Clutch sizes recorded were: Taitas: 3 eggs x 2; 4 eggs x 2 (in captivity 2 eggs x 4; 3 eggs x 27; 4 eggs x 2; mean = 2,9; W. Heck *in litt.*, pers. obs.); Peregrines: 2 eggs x 11; 3 eggs x 24; 4 eggs x 11 (in captivity 1 egg x 4; 2 eggs x 14; 3 eggs x 70; 4 eggs x 34; mean = 3,1 eggs; pers. obs.), and Lanners: 2 eggs x 2; 3 eggs x 30; 4 eggs x 38; 5 eggs x 2. Although mean clutch size for Taitas is 3.5 eggs, the sample size is small and the much larger sample for captive birds may be more realistic at 2.9 eggs, similar to the Peregrine (mean = 3), while the versatile Lanner had predictably the largest (mean = 3.55).

Table 6. Selected morphometrics of Taita, Peregrine and Lanner Falcons in Zimbabwe.

Morphometric	Species and sex, morphometric, S.D.(n)					
	Taita		Peregrine		Lanner	
	male	female	male	female	male	female
Weight (g)	219.9	312.9	495.0	700.5	474.9	607.1
	8.8(7)	24.0(9)	35.7(8)	105.8(14)	51.7(20)	56.0(9)
Bill length (mm)	13.5	13.5	19.3	27.3	19.1	20.8
	0.6(5)	1.4(9)	1.7(8)	0.8(14)	1.0(20)	0.4(9)
Bill width (mm)	13.1	14.0	15.7	18.1	15.8	16.2
	0.3(5)	0.6(9)	0.5(8)	0.9(14)	0.0(1)	0.0(1)
Gape (mm)	21.2	23.3	20.5	30.4	29.0	30.6
	0.3(5)	1.2(7)	5.1(8)	1.32(14)	0.0(1)	0.0(1)
Wing (mm)	207.4	235.6	277.3	324.4	314.0	347.0
	4.4(7)	5.0(9)	5.5(8)	9.4(14)	12.3(20)	13.7(9)
Tail (mm)	94.0	106.5	129.8	153.3	164.8	183.6
	4.9(5)	6.1(9)	5.2(8)	10.1(14)	10.1(20)	9.4(9)
Tarsus (mm)	30.2	31.3	43.2	45.1	46.5	47.2
	1.0(5)	0.8(9)	1.9(8)	2.7(14)	3.0(20)	0.8(9)
Mid-toe (mm)	34.1	35.0	47.0	50.9	41.8	45.5
	1.7(5)	0.9(9)	3.4(8)	1.6(14)	2.5(20)	2.7(9)
Wing area (cm²)	427.8	558.8	756.3	1044.8	1154.1	1286.3
	29.2(3)	59.1(6)	53.2(8)	63.8(9)	50.2(5)	108.2(3)
Wing loading (g/cm²)	0.51	0.56	0.61	0.71	0.42	0.48
	0.03(3)	0.09(6)	0.04(8)	0.05(9)	0.04(5)	0.04(3)

3. Morphology, hunting and prey

Taitas and Peregrines are very similar in structure (Table 6), feather texture and hunting behaviour, being especially adapted to fast, attacking flights at flying birds. Both have high wing loadings, short tails and big feet. Tail/wing ratios for Taitas, Peregrines and Lanners were 45%, 47% and 52%

respectively. Taitas and Peregrines also have shorter and harder feathers, probably contributing to their superior speed.

For its size, the Taita has a particularly high wing loading, and its wing beat is fast. This suits its style of short vigorous hunts close to the nest site (Hartley *et al.* 1993). Its bill is strong with a width:length ratio of 1.0 (Peregrines = 0.81; Lanners = 0.8) so that prey can be immobilised quickly, while there is little size difference in the bill size of males and females. Furthermore the gape is large relative to its size (*contra* Peregrine and Lanner; Table 6), and this probably facilitates quick consumption of food.

The Taita and Peregrine are markedly different in mass, females of the former weighing just 44.7% of the latter to give a character ratio (larger/smaller, Hutchinson 1959) of 2.24. Ratios for selected linear measurements between these species are 2.02 (bill length) and 1.38 (wing length). Such ratios between Lanner and Taita are 1.94 (mass), 1.54 (bill length) and 1.47 (wing length). Those for Peregrine and Lanner are 1.15 (mass), 1.31 (bill length) and 0.93 (wing length). Taitas and Peregrines also have big feet (mid-toe:tarsus ratios of 1.13 and 1.11 respectively) which facilitate capturing prey on the wing, contrasting with the smaller feet of Lanners (mid-toe:tarsus ratio of 0.93) which also take prey on the ground, including mammals and reptiles.

Table 7. Taxonomic groups of avian prey recorded for Taita (T), Peregrine (P) and Lanner (L) Falcons in Zimbabwe.

Family/group	No. (%)			% By weight		
	T	P	L	T	P	L
Columbidae	2 (3.1)	175(39.0)	52(54.7)	8.4	48.7	73.7
Phasianidae		12(2.7)	4 (4.2)		12.9	9.3
Apodidae	4 (6.2)	21 (4.7)	6 (6.3)	6.7	1.2	0.4
Hirundinidae	10(15.6)	7 (1.6)		8.5	0.4	
Sturnidae	6 (9.4)	42 (9.4)	1 (1.1)	30.9	5.5	0.8
Coraciidae & Phoeniculidae		22(4.8)			3.0	
Bucerotidae		21 (4.7)	1 (1.1)		6.9	1.0
Ploceidae	14(21.9)	38 (8.5)	2 (2.1)	13.2	1.6	0.4
Estrildidae	8(12.5)	11 (2.4)	4 (4.2)	3.9	1.0	0.4
Other passerines	17(26.6)	28 (6.2)	6 (6.3)	15.6	2.8	1.5
Other near-passerines	1 (1.6)	41 (9.1)	4 (4.2)	10.8	7.8	3.1
Other non-passerines	1 (1.6)	31 (6.9)	2 (2.1)	2.0	8.2	0.8
Domestic poultry & budgerigars			13(13.7)			8.6
Total	64 (100)	449 (100)	95 (100)	100	100	100

Of 30 prey species taken by Taitas (mean prey mass = 40.9 g), 15 were also recorded for Peregrines (mean prey mass = 139.7 g; 79 species) and it is likely that the latter can capture all prey taken by the former. Key prey overlap by taxonomic grouping included Apodidae, Hirundinidae, Ploceidae, Estrildidae and Sturnidae (Table 7). Four species taken by Taitas were also taken by Lanners (mean prey mass = 185.7 g; 30 species), although this is likely to be an underestimate. Sixteen prey species taken by Peregrines were also taken by Lanners. Being roughly 45% the mass of the Peregrine and Lanner, the Taita specialises on smaller birds which tend to be taken close to the nest using either still-hunting from a high vantage, speculative-hunting or hunting from a soar (Hartley *et al.* 1993). Coupled with the relatively high wing loading and the presumed extra energy costs, the Taita is constrained to a smaller home range, as little as 1 km radius around the nest during the breeding season (Hartley *et al.* 1993) and 45.6% of prey (by weight) was taken from cliff habitats (Table 8). However, at four sites that were abandoned, Taitas were not seen hunting near the nest cliffs where there was a paucity of prey, but rather these pairs relied mainly on woodland habitats. Three of these woodlands had declined through elephant damage, making them a less than optimum circumstance for this species.

Table 8. Habitat preferences of avian prey for Taita (T), Peregrine (P) and Lanner (L) Falcons in Zimbabwe.

Habitat	No. of birds (%)			% by weight		
	T	P	L	T	P	L
Cliff	20(31.2)	51(11.4)	2(2.1)	45.6	9.9	2.9
Woodland	40(62.5)	379(84.4)	47(49.5)	49.5	83.0	35.6
Grassland	3(4.7)		3(3.1)	4.9		0.9
Aquatic		18(4.0)			6.5	
Human ^a		1(0.2)	43(45.3)		0.6	60.6
Other	1(1.6)					
Total	64	449	95	100.0	100.0	100.0

^a feral and domestic pigeons *Columba livia*, poultry and budgerigars.

Taitas, Peregrines and Lanners all hunt significantly in woodland habitats for birds (Table 8), while the latter two also preyed significantly on columbids (Table 7). Ecological similarity between Taitas and Peregrines is supported by their similar hunting habits and vocalisations (Hartley *et al.* 1993). It is also supported by habitat preferences for prey, with woodland species dominating both by number and weight (Table 8), even more so than for the Lanner which has adapted well to human habitats (towns and cleared farmlands) and which took little prey from cliff habitats. However, the degree of use of these habitats was significantly different between Taitas and Peregrines ($\chi^2 = 19.8$, $P = <0.001$; cliff, woodland and other) and between Peregrines and Lanners ($\chi^2 = 216.01$, $P = <0.001$; cliff, woodland, human and other). Furthermore, Peregrines are much less dependent on cliff habitats than Taitas and have been seen hunting over woodland up to 30 km from their breeding sites. There was also a significant difference between prey selection (based on taxonomic grouping) between Taitas and Peregrines ($\chi^2 = 8.27$, $P = <0.001$) and between Peregrines and Lanners ($\chi^2 = 76.22$, $P = <0.001$).

4. Interspecific behaviour

There are three records of aggressive encounters between Peregrines and Lanners, all at cliffs shared for breeding. An encounter between two females in front of a Peregrine site degenerated into a tussle on a ledge, after which the Peregrine drove off the Lanner in a powerful aerial display. Peregrines were clearly dominant in the other interactions. Peregrines also pursued Taitas near the nest (Hartley *et al.* 1993). Away from the nest, Taitas and Peregrines have been seen soaring together without any interaction.

Peregrines killed small raptors such as Littlebanded Goshawk *Accipiter badius*, Blackshouldered Kite *Elanus caeruleus* and Barn Owl *Tyto alba* (pers. obs.). Under falconry conditions, it is not unusual for trained Peregrines to attack small raptors, and other species so killed included Gabar Goshawk *Micronisus gabar*, Ovambo Sparrowhawk *A. ovampensis*, Hobby *F. subbuteo*, Eastern Redfooted Falcon *F. amurensis*, Pearl-spotted Owl *Glaucidium perlatus* and Marsh Owl *Asio capensis*. Trained Lanners also attacked and killed Barn and Marsh Owls.

All three species attack eagles that venture within 200-300 m of their nests. Taitas also attack hornbills, presumably because the latter could rob eggs and chicks (Hartley *et al.* 1993). Lanners appear to be particularly aggressive to nesting eagles, in order to commandeer their nests which they appear to do on occasions. Taitas and Peregrines were much less drawn to old stick nests and there are no records of them commandeering such nests. Along extensive cliff systems, Peregrines appear to avoid breeding near active Black Eagle nests.

Barn Owls probably compete with these falcons for nest holes and several Barn Owls have been recorded as Peregrine prey (pers. obs.). However, the remains of an adult male and female Peregrine were found about 500 m away from their nest hole in the nest hole of a Mackinder's Eagle Owl *Bubo capensis mackinderi* (F. Couto pers. comm.). Barn Owls have been flushed from cavities frequented by Taitas and it is possible that these owls could kill these much smaller falcons at night.

DISCUSSION

Status and distribution

There is no information on internest distances for Taitas, apart from Moller (1989), Dowsett (1983) and this study, and it appears that there is some clustering of sites in areas with extensive cliff systems. A 70 km-long cliff system on Mt. Elgon, Uganda, hosted 19 pairs of Peregrines, 5 pairs of Lanners and 4 pairs of Taitas (Moller 1989), the ratio of Peregrines to Taitas being similar to the Zambezi Valley. Otherwise, distribution of Taitas is very patchy (see also Hunter *et al.* 1979). By contrast, Peregrines can occur at relatively high densities and those in Batoka Gorge, parts of the Sebungwe valley and in the Save system exceeded that recorded in the Waterberg Plateau of Namibia (mean = 5.1 km/nest; Brown & Cooper 1987) and parts of the eastern escarpment of South Africa (mean = 7.5 km/nest; A.R. Jenkins & T. Wagner *in litt.*). Particularly dense clusters of Peregrines in Zimbabwe (two sites 0.35 km apart and three sites 1 km and 1.7 km apart) match that recorded by Thomsett (1988) in Kenya.

Where there was competition in domed inselberg terrain with Lanners, internest distance increased significantly for Peregrines in Zimbabwe, again in accord with estimates from Kenya by Brown & Amadon (1968) and Thomsett (1988), but double that recorded in the south-western Cape (Pepler *et al.* 1991).

On the granite shield and in three zones with high densities of quarries, Lanner Falcons occurred at comparable densities to those recorded in South Africa (8.6–9.5 km/nest; Tarboton & Allan 1984), Namibia (4 km/nest; Brown & Cooper 1987) and Zambia (3.5 km/nest; Osborne & Colebrook-Robjent 1984).

Comparative ecology

That Taitas and Peregrines shared similar ecological conditions, and that Taitas were sympatric with Peregrines, is also supported by observations in Uganda (Moller 1989), Kenya (Thomsett 1988), South Africa (Jenkins 1991), Zambia and Malawi (Hunter *et al.* 1979). In South Africa, a pair of Taitas bred in an old Peregrine site on an escarpment (Jenkins 1991), near a gorge which has had up to 4 pairs of Peregrines (Tarboton & Allan 1984). Taitas and Peregrines were also found in granitic domed inselberg terrain in the miombo woodlands along the Muchinga Escarpment of Zambia (J. Weaver pers. com.; J. Auburn *in litt.*) and Mwanza district of Malawi (Hunter *et al.* 1979; J. Auburn *in litt.*). Specimens of Taitas have been recovered near granite terrain at Mt. Darwin (Smithers 1956), Nyanga Downs (Snell 1963) and near Mutare (Black 1983).

Although Peregrines were tied to cliff habitats in woodlands in Zimbabwe (Hustler 1983; Thomson 1984; Hartley 1992), Zambia (Osborne & Colebrook-Robjent 1980), the Transvaal (Tarboton & Allan 1984) and Namibia (Brown & Cooper 1987), a significant population (48–95 pairs; Pepler *et al.* 1991) occurred in the fynbos of the south-western Cape. Pairs have also occurred in desert landscapes, on cliffs overlooking a water hole (Braby *et al.* 1987) and along Fish River (Maclean 1960) in Namibia, and along the lower Orange River in South Africa (Jenkins & Van Zyl 1994). In each of these areas, Peregrines have probably retained a competitive edge over Lanners because most available prey can only be hunted consistently by aerial hunting (Thomson 1984; Brown *et al.* 1987; Jenkins 1995).

The ultimate factors for Peregrines were cliffs and suitable numbers of avian prey, while proximate factors were raised canopies (woodlands and fynbos, Jenkins 1994) and water (to attract avian prey), which could be exploited by their aerial hunting techniques. River valleys can also function as corridors for prey (Hartley 1992), suiting these specialised aerial attackers. Although Taitas, Peregrines and Lanners all used small cliffs in Zimbabwe, contrasting ecological requirements, especially between Peregrines and Lanners, limited competition for these sites. Taita and Peregrine sites were primarily in woodland habitats, positioned over significant river systems with permanent water nearby, either in the river and/or in a spring. This was always the case for small cliffs (Fig. 2), several overlooking permanent springs and/or close to river junctions. By contrast, Lanners occurred at lower densities in these areas and their numbers may also have been restricted by the limited variety and abundance

of prey, and by competition for nest sites with the Peregrine. Furthermore most Lanner sites on small cliffs were in more open habitats and were not linked either to woodland or water. Peregrines and Lanners also bred on buildings and in quarries.

Cliff heights used by Peregrines and Lanners in Zimbabwe compared with patterns elsewhere (Tarboton & Allan 1984; Mendelsohn 1988), where Peregrines occupied significantly more dominant features than Lanners. However, in Zimbabwe (as on the Waterberg Plateau, Namibia) smaller cliffs were used more frequently by Peregrines than elsewhere in Africa, especially South Africa (Tarboton & Allan 1984; Mendelsohn 1988; Pepler *et al.* 1991). This is probably because where there is a good food supply less desirable nesting cliffs may be accepted (Hustler 1983; Brown & Cooper 1987), and walk-on sites have also been recorded in Kenya (Thomsett 1988). The hypothesis that Peregrines benefit on an energy/time-cost basis by selecting high cliffs has been discussed by Tarboton (1984), Thomsett (1988), Newton (1988) and Jenkins (1995). Taitas would benefit in the same way from using high cliffs, which were also the most consistently occupied features in Zimbabwe. Energy constraints, from high wing loading and relatively small size, may influence more efficient hunting near cliffs by increasing costs for efforts made further afield, especially during the breeding season when increased provisioning is necessary. It is also possible that competition with the Peregrine means that the smaller falcon is constrained to accept the least optimum cliffs. This is supported by studies in Namibia, where Rock Kestrels *F. tinnunculus* occupied the smallest cliffs, after Lanners and Peregrines (Brown & Cooper 1987).

In the Transvaal, Peregrines and Lanners avoided west, north-west and south-west aspects for their nests (Tarboton & Allan 1984). By contrast, in Zimbabwe 47% Taita, 30% Peregrine and 35% Lanner nests were on these aspects (Table 4). Tree nesting has also extended the range of Lanners into more open woodland areas without cliffs, where there is no overlap with nesting Peregrines. Lanners used stick nests more frequently than the other two species and patterns accord generally with the Transvaal (Tarboton & Allan 1984). While Gargett (1990) described both Lanners and Peregrines using old Black Eagle nests, there were no records of Lanners attempting to oust Black Eagles from their nests. Few pylon sites were used (contra 22.3% in the Transvaal; Tarboton & Allan 1984), probably owing to weaker observer effort in this context in Zimbabwe, and possibly also to the greater frequency of larger trees with old eagle nests. Owing to their morphology, Lanners are generalists with an encompassing range that breed in a great variety of sites. Consequently, they are usually the most numerous of the three species, especially today with increasing human-modified landscapes.

The rarity of the Taita is probably determined by its more specialised habitat requirements, and possibly also by its interspecific relationship with the Peregrine (Thomson 1984; Hustler 1989; Hartley *et al.* 1993), while the Lanner is generally an open country species whose range has probably increased with recent deforestation in Africa (Thomson 1984). Notwithstanding their similarities, key differences in ecomorphology have probably allowed Taitas and Peregrines to co-exist. Character ratios of mass, bill and wing lengths all exceed 1.3, and so minimise overlap. Similar contrasts were seen in three North American accipiters (Storer 1966, in Wiens 1992). These body-size relationships also correspond with differences in both the range and mean of prey sizes taken by Taitas and Peregrines, suggesting that some minimal morphological separation is necessary to permit the co-existence of congeners (Wiens 1992). The large linear bill:length ratio for Taitas and Peregrines is consistent with the findings of Schoener (1965, in Wiens 1992) for food specialists using foods of relatively low abundance, which also translates into species whose body sizes are large relative to overall food abundance. Such differences in size in Taitas and Peregrines may have arisen to make foraging more effective (optimal foraging; Dodson *et al.* 1998), rather than competitive. Peregrines can take a much wider range of prey, from small to medium-sized birds, and can take them at much further distances from the nest, than is cost effective for Taitas. It is likely that Taitas are more agile and better adapted to taking cliff-dwelling species and small birds in close proximity to their nests.

Indeed the Taita is more specialised than the Peregrine, with its apparently greater dependance on cliff habitats for prey and its smaller home range during the breeding season. It is apparent that the Taita has a narrower niche than the Peregrine and Lanner and so is less successful numerically.

Less consistent nesting was recorded for the Taita on small cliffs, where it depended primarily on woodland habitats and was probably forced to hunt further afield. Outside the breeding season, in common with Peregrines and Lanners, Taitas may also move away from cliff habitats in search of food (Britton 1980; Muller 1989), although this has not yet been recorded in Zimbabwe.

Similarly large character ratios typify Taitas and Lanners, while for Peregrines and Lanners only the bill:length ratio exceeds 1.3. Instead, wing shape, wing beat, wing loading and foot size contrast more significantly for Peregrines and Lanners (Jenkins 1995), producing contrasts in hunting methods and so reducing competition. Lanners are better adapted for soaring in thermals and so they possibly hunt for longer periods during the day, at different times to Taitas (Hartley *et al.* 1993), and to Peregrines which tend to be more crepuscular (Ratcliffe 1980; Hustler 1983; pers. obs.). By contrast, the more specialised Taita and Peregrine are better adapted than the Lanner at making fast attacking flights at flying birds, especially from cliffs overlooking wooded valleys. In these zones, the Peregrine may restrict the Taita, and can outcompete the Lanner whose ground-hunting opportunities are limited. High wing loadings of Taitas and Peregrines probably hinder their ability to hunt prey on the ground, and they probably expend proportionately more energy in flight than the more buoyant Lanners with their significantly lower wing loading.

Lanners can search more effectively (Jenkins 1995) and use a greater variety of hunting methods (Thomson 1984; Yosef 1991; Jenkins 1995), including successful attacks on ground prey such as rodents, locusts, reptiles and poultry, while smaller feet and longer tails assist this generalist. As they can soar more easily, Lanners are less dependent on high cliffs and consequently are better adapted than the other two species in relatively featureless terrain. Hence, Lanners can outcompete the other two species in more open habitats, especially when the number and range of avian prey is depressed (see also Jenkins 1994, 1995). Furthermore, Lanners have adapted to hunting poultry around kraals and settlements (Steyn 1982; Barbour 1971; Hartley *et al.* 1995), supporting the contention that they have been replacing Peregrines over areas in the high- and middleveld where there has been extensive clearance of land for agriculture (Thomson 1984).

Birds comprised 79% of Lanner prey in the Transvaal (Kemp 1993) and 78.5% in Israel (Yosef 1991), a similar proportion to this study. Domestic pigeons were taken commonly in towns (Mendelsohn 1988) and wild columbids comprised 43% of prey for pylon-nesting Lanners in the Transvaal (Kemp 1993). In Botswana, outside of the breeding season, Redbilled Quelea were also key prey for the migrant Lanners which occurred there, mainly from October-February (Herremans & Herremans-Tonnoeyr 1996) as opposed to March-June in Zimbabwe (Hartley 1998). It is possible that they move north during the winter and that this population breeds elsewhere in Africa (Herremans & Herremans-Tonnoeyr 1996). The significant difference in prey taken by Taitas, Peregrines and Lanners, both by habitat and by taxonomic grouping, is not surprising. It reduces competition and allows the presence of at least two species in many areas, while competition for breeding sites probably ultimately restricts the Taita.

In tropical woodlands, especially in the wet season, there can be significant avian abundance (Vernon 1985) that is enhanced by the inclusion of islands of non-miombo habitat, including: 1) the cliff habitat; 2) the contrasts above and below breeding cliffs, especially along escarpments (Zambezi valley = miombo above cliffs and mopane woodlands below); and, 3) habitats along rivers and their terraces with more nutrient-rich soils and water. In such areas, Lanners only breed where there were openings caused by elephant damage or, latterly, by human encroachment and clearance for cultivation.

Immigration of Lanners probably increases competition for nest sites (Moller 1989) and, being the smallest and most specialised, the Taita probably loses. This trend is supported in this study (Sebungwe), the Muchinga Escarpment of Zambia where Lanners now breed at 3/4 sites where Taitas used to nest, and in Malawi where Taitas seem to be absent from both areas where the species was known to occur in the late 1970's (J. Auburn *in litt.*). In 1983, J. Weaver (pers. comm.) commented on the start of land degradation along the Muchinga Escarpment, where a pair of Peregrines and Taitas nested successfully on the east faces of separate inselbergs 2 km apart. The same has probably occurred in the degraded inselberg terrain around Mt. Darwin (Zimbabwe) where a Taita was collected (Smithers 1956).

By contrast, patchiness of certain habitats, as caused by cultivated lands for cereals in a mosaic of intact woodlands, may have assisted both Peregrines and Lanners which can hunt the local abundance of columbids and queleas. This may also have allowed Peregrines to occupy breeding sites for longer periods and be in position before, or at the same time, as Lanners. This appears to be the case on General Land in zone 2 where Peregrines have maintained fidelity to nest sites, while in neighbouring Communal Lands there were frequent nest changes with Lanners, probably owing to the circumstances, improved for the latter and declining for the former.

Deforestation has probably reduced avian prey diversity and abundance for Peregrines, which have to spend longer periods hunting and at further distances from the dominant cliff sites which still attract them. Consequently, Lanners can more easily occupy some of the Peregrine breeding sites. By contrast, in woodland habitats of the Zambezi and Save valley systems, Peregrines appear to be resident all year round. These circumstances indicate contrasting ecological conditions which favour one species and are detrimental to the other respectively, and are not examples of competition.

Since 62% of Peregrines (Table 2) were found breeding in intact and relatively intact habitats, on State and private land respectively, coupled with their competitive edge over Lanners in these habitats, the breeding season did not appear to be a critical factor determining their respective population status in Zimbabwe (*contra* Thomson 1984). Site requirements (Thomson 1984; Mendelsohn 1988) have probably been more decisive, influenced by morphology, hunting behaviour and prey of the falcons (Jenkins 1995).

Laying dates for Peregrines and Lanners accord with Irwin (1981) and Tarboton & Allan (1984). However, the June and July laying dates for Taitas in Irwin (1981) appear to be incorrectly assigned (Hartley *et al.* 1993). Peak laying dates for Taitas and Peregrines appear to coincide with peak abundance of prey when the young are flying (Olsen & Georges 1993), while the earlier peak laying date for Lanners appears to coincide with the period of lowest cover and highest availability of insects during the start of the rains in October-November. Lanners are better adapted than Taitas and Peregrines at hunting these on or just above the ground, and juveniles especially can take advantage of these circumstances soon after fledging.

Young passerines fledge from mid-November onwards, by which time most migrants have also arrived, and this should suit juvenile Taitas and Peregrines. Taitas laid, on average, 21 days later than Peregrines nesting in the same vicinity. This may be to avoid any contact when the Peregrines are displaying (Hartley *et al.* 1993), since they are aggressive around the nest at this time. Taitas then intensify their breeding activity when the Peregrines are incubating and at their most discreet and unobtrusive (Hartley *et al.* 1993).

Significant interspecific competition for nests was recorded in Kenya (Thomsett 1988) and the Transvaal (Tarboton & Allan 1984). The only other record of predation by an owl also involved a Mackinder's Eagle Owl (which took a juvenile Lanner; Steyn & Tredgold 1977). However, this was a significant problem in the USA where Great Horned Owls *Bubo virginianus* attack Peregrines (Cade 1982).

Pesticides do not appear to be a significant problem in Zimbabwe (Hartley 1993c; Hartley *et al.* 1995; Hartley *et al.* 1996), but habitat destruction has been rapid (Whitlow 1980a & b, 1988) and the policy of land acquisition threatens to accelerate this trend (Sill 1992). Habitat destruction could result in the displacement of Taitas by Lanners, and Lanners could also extend their range at the expense of Peregrines. Monitoring of Taitas, Peregrines and Lanners, with respect to habitat quality in the three land-use categories, should be continued.

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R.R. Hartley
Zimbabwe Falconers' Club
Falcon College
Esigodini
Zimbabwe

