

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

ANDREW R. JENKINS

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

Peregrine Falcon *Falco peregrinus* 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. Foraging mode varied considerably between sites, and males foraged more actively than females but there was little variation in the design of hunts between sexes, seasons or study areas. Individually, Peregrines spent 30–50% of the day on or near the nest cliff. On average, about 0.5 hunts were recorded per hour of observation. Foraging mode was not correlated with cliff height or elevation above the surrounding terrain, but Peregrine pairs occupying higher cliffs achieved greater 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 positively and 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.

The Peregrine Falcon *Falco peregrinus* is a morphologically and behaviourally specialized predator of birds (Cade 1982, del Hoyo *et al.* 1994, Jenkins 1998). 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).

I describe the foraging behaviour of Peregrines in South Africa. African Peregrines *F. p. minor* are non-migratory, and the activities of territorial pairs are centred on the nest cliff throughout the year (Mendelsohn 1988, Jenkins 1994). In many areas, resident pairs are restricted to particularly high cliffs (e.g. Tarboton & Allan 1984, Jenkins 1994) which are rare in 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 a prerequisite for successful breeding in African environments (Tarboton 1984, Jenkins 1991). Two predictions of this hypothesis are examined here: (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 1989–96 at eight sites on the Cape Peninsula, Western Cape Province (34°10'S, 18°25'E), four sites along the lower Orange River, Northern Cape Province (28°30'S, 17°00'–20°40'E) and four sites in the Soutpansberg range, Northern Province (23°00'S, 29°40'E). Three of the Cape Peninsula sites were on low to moderate cliffs with steep scree slopes, overlooking a mosaic of urban, forest and heathland

Email ajenkins@botzoo.uct.ac.za

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. This is a hilly to mountainous area, sparsely vegetated except for narrow strips of riparian bush or irrigated croplands along the river banks. 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 10 × 40 binoculars or a 20–60× 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.

In total, 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 (Appendix 1). Observation periods were classified 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 (octets), temperature (cool, mild or warm-hot) and wind strength (calm-light, light-moderate, moderate, moderate-strong or strong) and direction (compass octants). The earliest 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 (i.e. within sight of the observer) 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 hunt was seen, each hunting attempt/strike was summarized by up to 15 variables (Appendix 2). 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 classified according to a subjective assessment of 'intensity' (see Treleaven 1980). 'High intensity' hunts were typically preceded by periods of alert scanning or 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.

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. *Columba* pigeons), and at the expense of longer strikes at typically low-flying prey (especially *Streptopelia* doves). This problem was particularly prevalent in the Soutpansberg where tall vegetation often hampered visibility.

Statistical analyses

The data generally were not normally distributed, so non-parametric statistical tests were used throughout. Analyses (and hence data presentation) were structured first to account for variation between sexes (within pairs), between seasons (within each study area) and between areas, before data were pooled to maximize sample sizes in the examination of environmental correlates of foraging behaviour and success.

Differences in cliff attendance, hunting rates of males and females of each pair, and seasonal differences in these parameters within individuals of each sex (only for sites with at least 50 h of observation per season), were examined using Wilcoxon paired-sample tests (Zar 1984). Kruskal–Wallis one-way ANOVA was used to examine within-sex differences between the three study areas, and variation between pairs within each area. Thereafter, data for all observation periods were pooled.

Initial analyses of data describing hunts were restricted to individuals or pairs hunting together for which samples of ten 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. Means 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, 2350.7 bird-hours of observation were accumulated (Appendix 1), 941.4 h for males and 1409.3 h for females. A total of 1318 hunting attempts

was observed, 372 by males alone, 821 by females and 125 were by both members of the pair (Appendix 1).

Variation between sexes, seasons, sites and study areas

Females were present at the nest cliff for a greater proportion of each observation period than males (Table 1a) and more hunts by females were seen per hour of observation than by their mates (Table 1a). Males showed no seasonal variation in cliff attendance, but hunted in the vicinity of the nest cliff (i.e. within an observable distance) more frequently in the breeding season (Table 1b). 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 1c), although sample sizes were small and average hunting rate figures were quite different in some cases. There was significant variation in cliff attendance and hunting rates of pairs between sites in each study area (Table 2). 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 small birds relatively more frequently than their mates, and pairs hunted smaller birds in larger flocks than Peregrines hunting alone (Tables 3 & 4). Also, pairs made high intensity strikes relatively more frequently than individuals (Table 4). Otherwise, hunts by males vs females of pairs, and by individuals within pairs vs pairs hunting together, did not differ significantly for most variables (Tables 3 & 4). Overall, males made relatively more strikes at birds in flocks (as opposed to isolated individuals) than females (males 40.1% of 372 hunts vs females 33.0% of 821 hunts, χ^2_1 with Yates' correction = 5.27, $P = 0.02$). Males and females achieved equal success in strikes at small birds (males 51.7% of 58 hunts vs females 46.4% of 28 hunts, $\chi^2_1 = 0.05$, $P = 0.82$), 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 2).

Table 1. 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 (a) males and females of pairs, (b) breeding and non-breeding seasons for birds of each sex and (c) the three study areas for birds of each sex.

(a)	Males	Females	Wilcoxon Z	
Pairs (<i>n</i> = 16)				
Attendance (%)	26.6	39.7	3.54***	
Hunts per hour	0.08	0.14	2.18*	
(b)	Breeding	Non-breeding	Wilcoxon Z	
Males (<i>n</i> = 5)				
Attendance (%)	38.7	36.5	0.54 ns	
Hunts per hour	0.25	0.12	2.16*	
Females (<i>n</i> = 5)				
Attendance (%)	49.1	48.3	0.54 ns	
Hunts per hour	0.30	0.29	0.27 ns	
(c)	Cape Peninsula	Orange River	Soutpansberg	Kruskal–Wallis <i>H</i>
Males	(<i>n</i> = 8)	(<i>n</i> = 4)	(<i>n</i> = 4)	
Attendance (%)	25.7	30.8	24.2	0.42 ns
Hunts per hour	0.08	0.14	0.02	2.57 ns
Females	(<i>n</i> = 8)	(<i>n</i> = 4)	(<i>n</i> = 4)	
Attendance (%)	36.1	44.0	42.7	1.61 ns
Hunts per hour	0.18	0.14	0.06	4.20 ns

P* < 0.05, **P* < 0.001.**Table 2.** Estimates of the height and elevation above the surrounding terrain 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

Table 3. Average data (with ranges in parentheses) comparing hunts by males and females of Peregrine pairs ($n = 5$ pairs).

Variable	Males		Females		Wilcoxon Z
Hunts from a perch (%)	66.8	(50.0–78.2)	65.2	(58.3–72.5)	0.27 ns
Hunts at flying birds (%)	78.3	(61.1–91.1)	64.8	(33.3–89.2)	1.62 ns
Perch/flying height (m)	150	(78–284)	155	(73–332)	0.27 ns
Distance to prey (m)	355	(265–535)	369	(247–456)	0.54 ns
Prey height ground (m)	70	(49–134)	74	(40–139)	0.54 ns
Relative height (%)	80.4	(65.0–88.8)	82.8	(80.0–85.9)	0.27 ns
Height difference (m)	85	(33–142)	88	(32–203)	0.27 ns
Hunts of 'high intensity' (%)	33.5	(20.2–70.0)	24.2	(15.4–30.8)	0.81 ns
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 ns
Success (%)	21.2	(0.0–70.0)	15.5	(7.7–23.1)	0.81 ns

See Appendix 2 for full definition of each variable.

* $P < 0.05$.

Use of the nest cliff

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 2).

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. 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. In a sample of full-day watches at active sites ($n = 15$), breeding pairs made an average of 4.9 strikes per day (range 0–16) at birds in the immediate vicinity of the nest cliff, and successful hunts accounted for 21.4% (range 0–56%) of all prey delivered to nests.

There were no significant correlations between foraging mode and prevailing weather conditions (cf. Jenkins 1995), although cliff attendance tended to decrease with increasing wind strength ($r_s = -0.90$, $n = 5$ wind categories, 1761 observation periods, $P = 0.07$), suggesting that Peregrines may have extended their foraging ranges on windy days.

Table 4. Average data (with ranges in parentheses) comparing hunts by individual Peregrines and hunts by pairs ($n = 4$ sites).

Variable	Individuals		Pairs		Wilcoxon Z
Hunts from a perch (%)	64.5	(56.0–72.6)	73.5	(66.0–83.3)	1.28 ns
Hunts at flying birds (%)	72.0	(55.5–89.50)	94.2	(88.2–100)	1.64 ns
Perch/flying height (m)	173	(91–310)	182	(82–346)	0.36 ns
Distance to prey (m)	372	(250–489)	416	(271–588)	0.91 ns
Prey height (m)	89	(60–137)	103	(28–218)	0.80 ns
Relative height (%)	81.8	(74.1–86.4)	83.9	(79.4–89.2)	1.28 ns
Height difference (m)	116	(32–179)	97	(34–154)	0.27 ns
Hunts of '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 ns

See Appendix 2 for full definition of each variable.

* $P < 0.05$.

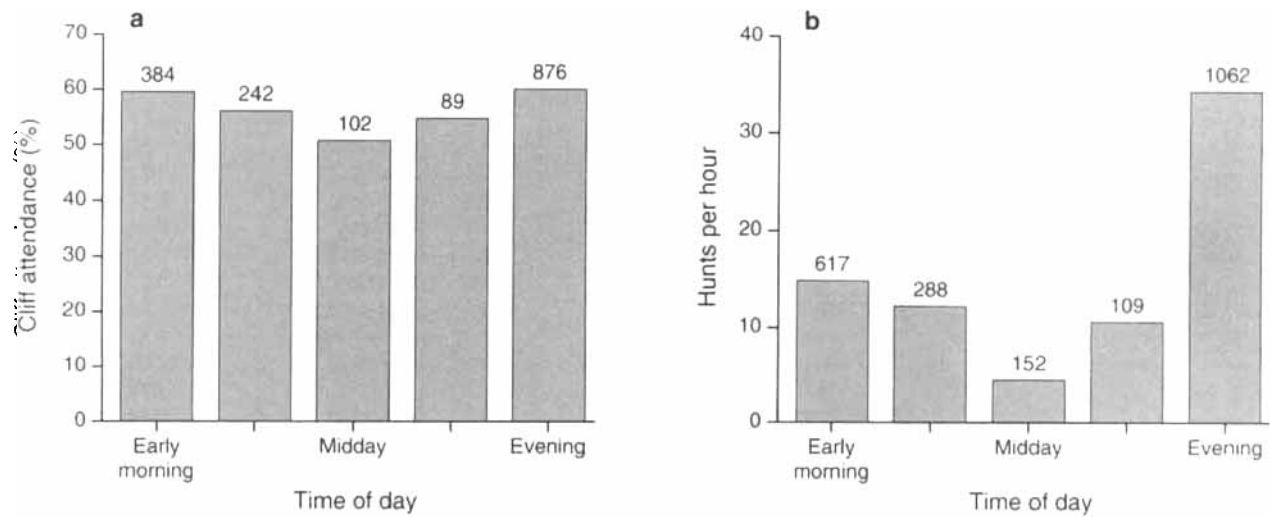


Figure 1. Peregrine cliff attendance (a) and hunting rates (b) in relation to time of day. The number of observation periods completed (a) and the number of hours of observation accumulated (b) for each time period in the day are indicated at the top of each bar.

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 levelled off 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. Peregrines 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 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 and chase 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 above the surrounding terrain ($r_s = -0.30$, $n = 16$, $P = 0.24$, data from Table 2). 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, $\chi^2_1 = 0.04$, $P = 0.84$). 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 *Streptopelia* doves and small passerines) more successfully than larger species (Table 5). Most exploratory, low-intensity hunts were made at particularly aerial or large prey species (e.g. swifts and *Columba* pigeons). Aerial insectivores, medium to large birds and *Columba* pigeons stayed airborne and outflow Peregrines in 93.5% ($n = 31$), 71.4% ($n = 21$) and 44.3% ($n = 183$), respectively, of unsuccessful hunts at these quarry. In contrast, *Streptopelia* 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 *Columba* pigeons) were more successful than hunts at flocks of two or more

Table 5. 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–large birds ^f	47	2.1	1.6	29.8	0.0

^aSmall columbids, low-flying, mostly *Streptopelia* sp.; ^bmostly sparrows and queleas; ^cmostly starlings and weavers; ^dswifts, swallows and martins; ^elarge columbids, high-flying, *Columba* sp.; ^fmostly ducks, small raptors and waders.

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 6). 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 6). 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. 2; $r_s = 1.00$, $n = 5$ height 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 perhaps only made at particularly vulnerable prey, hence Peregrines were relatively successful in these

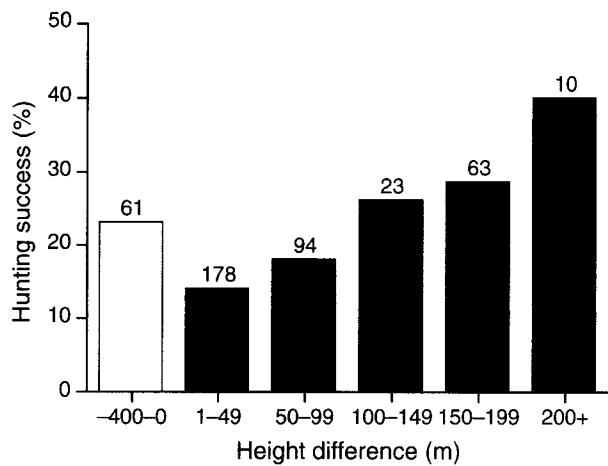


Figure 2. Peregrine hunting success in perch hunts in relation to the vertical height difference between falcon and prey at the start of the hunt. Sample sizes (number of hunts seen) for each height difference category appear at the top of each bar.

situations (Fig. 2) without the benefit of an initial height advantage, and the relationship between strike success and height difference was not significant if these hunts were included in the analysis (e.g. r_s for all strikes combined = 0.66, $n = 6$ height difference categories, 467 strikes, $P = 0.14$). Height difference was the only variable which differed significantly

Table 6. 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	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

See Appendix 2 for full definition of each habitat category.

between successful and unsuccessful strikes made directly downwards (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

Nesting habitat as a foraging area

Average cliff attendance and strike rate figures recorded during this study (Tables 1 & 2) confirm that South African Peregrines are relatively sedentary (also see Jenkins 1995) and make extensive use of the nest cliff and its surrounds (the nesting habitat) as a foraging area throughout the year. 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 probably 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 with cliff height. However, this study revealed no significant correlations between hunting mode and cliff height or elevation, possibly because only a small number of nest-sites was 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 the lower sites in each area (e.g. PA1, PB3 and PC5; Table 2) 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 higher sites at less food-rich localities (e.g. PA3, PB1 & PC2) foraged more actively and made fewer strikes close to the nest cliff. Also, pairs occupying particularly large cliffs were

more difficult to locate when present within the nesting habitat, so cliff attendance at these sites may have been underestimated.

The proportion of observed hunts initiated from perches on the nest cliff is typical of breeding pairs throughout the species' range (Table 7). In contrast, Peregrines 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 7). 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, Jenkins 1995). While wintering Peregrines may hunt more energetically, and their success rate is lower than that of breeding pairs (Table 7), they often hunt larger prey with much higher energy returns (e.g. Dekker 1980, 1995). Breeding pairs that regularly hunt from the nest cliff generally exploit aerial or 'commuter' prey species (e.g. columbids, migrants, aerial insectivores; Jenkins 1998). This complies with optimal foraging theory, which suggests that sit-and-wait predators should favour active, widely foraging prey (Huey & Pianka 1981).

Targets and tactics

The tendency for females to hunt larger birds than males (Table 3) was consistent 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 (Jenkins 1995) 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 for active co-operation between males and females in terms of accepted criteria, e.g. division of labour, communication to co-ordinate movements, sharing of prey (Hector 1986). Tandem hunts were particularly effective when

Table 7. 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 ^f	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

^aMonneret 1973, > 1 pair; ^bthis study, five pairs; ^cParker 1979, one pair; ^dSherrod in Cade 1982, one female; ^eThiollay 1988, five pairs; ^fBird & Aubry 1982, one pair; ^gTreleaven 1980, > 1 pair; ^hCade & Sherrod in Cade 1982, one male; ⁱRudebeck 1951, > 1 individual; ^jDekker 1980, > 1 individual; ^kClunie 1976, one adult female; ^lCresswell 1996, 8 individuals; ^mRuggiero 1991, one adult pair.

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.

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. Hence the results of this study may be biased by the inequality of sample sizes obtained from each site (see Appendix 1). It is hoped that this potential for bias was offset by a fairly conservative approach to data analysis and interpretation.

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 6) 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, Jenkins 1994).

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 above the surrounding terrain. 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 2 where cliff height is

less than 50% of elevation). Particularly long scree slopes provided elevation but did not provide vertical airspace adjacent 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. 2). 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 (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, breed more successfully (e.g. Mearns & Newton 1988, Jenkins 1998), and achieve higher rates of adult survival and lifetime reproductive success, than pairs on low cliffs.

I am grateful to Dave Allan, Zeldá Bate, Tim Wagner and Anthony van Zyl for their help in the field. South African National Parks kindly allowed me to work in the Au-grabies Falls National Park. The development of ideas presented here benefited greatly from discussion or correspondence with Dave Allan, Chris Brown, Rob Davies, Phil Hockey, Alan Kemp, Roy Siegfried, Rob Simmons and Anthony van Zyl. Helen de Klerk assisted with data analysis. Rob Davies, Morné du Plessis, Phil Hockey, Sarah Newman, John Quinn, Rob Simmons and an anonymous referee made useful comments on earlier drafts. This study was partly funded by the Foundation for Research Development.

REFERENCES

- Andersson, M. & Norberg, R.Å. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**: 105–130.
- Beebe, F.L. 1974. Field studies of the Falconiformes of the British Columbia: vultures, hawks, falcons, eagles. *British Columbia Prov. Mus. Occasional Papers* **17**: 1–163.
- Bird, D.M. & Aubry, Y. 1982. Reproductive and hunting behaviour in Peregrine Falcons *Falco peregrinus*, in Southern Quebec. *Can. Field Nat.* **96**: 167–171.
- Cade, T.J. 1982. *The Falcons of the World*. London: Collins.
- Cresswell, W. 1996. Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. *Ibis* **138**: 684–692.
- Ciunie, F. 1976. A Fiji Peregrine (*Falco peregrinus*) in an urban-marine environment. *Notornis* **23**: 8–28.
- Czechura, G.V. 1984. The Peregrine Falcon (*Falco peregrinus macropus*) Swainson in southeastern Queensland. *Raptor Res.* **18**: 81–91.
- Dekker, D. 1980. Hunting success rates, foraging habits, and prey selection of Peregrine Falcons migrating through Central Alberta. *Can. Field Nat.* **94**: 371–382.
- Dekker, D. 1995. Prey capture by Peregrine Falcons wintering on southern Vancouver Island, British Columbia. *J. Raptor Res.* **29**: 26–29.
- del Hoyo, J., Elliot, A. & Sargatal, J. (eds) 1994. *Handbook of the Birds of the World*, Vol. 2, *New World Vultures to Guinea-fowl*. Barcelona: Lynx Edicions.
- Hector, D.P. 1986. Cooperative hunting and its relationship to foraging success and prey size in an avian predator. *Ethology* **73**: 247–257.
- Huey, R.B. & Pianka E.R. 1981. Ecological consequences of foraging mode. *Ecology* **62**: 991–999.
- Hustler, K. 1983. Breeding biology of the Peregrine Falcon in Zimbabwe. *Ostrich* **54**: 161–171.
- Jenkins, A.R. 1988. Peregrines and high cliffs. *Ostrich* **59**: 78.
- Jenkins, A.R. 1991. Latitudinal prey productivity and potential density in the Peregrine Falcon. *Gabari* **6**: 20–24.
- Jenkins, A.R. 1994. The influence of habitat on the distribution and abundance of Peregrine and Lanner Falcons in South Africa. *Ostrich* **65**: 281–290.
- Jenkins, A.R. 1995. Morphometrics and flight performance of southern African Peregrine and Lanner Falcons. *J. Avian Biol.* **26**: 49–58.
- Jenkins, A.R. 1998. Behavioural ecology of Peregrine and Lanner Falcons in South Africa. PhD thesis, University of Cape Town, Cape Town.
- Jenkins, A.R. & van Zyl, A.J. 1994. Flush-hunting and nest robbing by Peregrine Falcons. *J. Raptor Res.* **28**: 118–119.
- Lazarus, J. & Symonds, M. 1992. Contrasting effects of protective and obstructive cover on avian vigilance. *Anim. Behav.* **43**: 519–521.
- Mearns, R. & Newton, I. 1988. Factors affecting breeding success of Peregrines in south Scotland. *J. Anim. Ecol.* **57**: 903–916.
- Mendelsohn, J.M. 1988. The status and biology of the Peregrine in the Afrotropical Region. In Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. (eds) *Peregrine Falcon Populations: their Management and Recovery*: 297–306. Idaho: The Peregrine Fund.
- Monneret, R.-J. 1973. Techniques de chasse du Faucon Pèlerin *Falco peregrinus* dans une région de moyenne montagne. *Alauda* **41**: 403–412.
- Parker, A. 1979. Peregrines at a Welsh coastal eyrie. *Br. Birds* **72**: 104–114.
- Ratcliffe, D.A. 1993. *The Peregrine Falcon*. London: T. & A.D. Poyser.
- Roalkvam, R. 1985. How effective are hunting Peregrines? *Raptor Res.* **19**: 27–29.
- Rudebeck, G. 1951. The choice of prey and modes of hunting of predatory birds with special reference to their selective effects. *Oikos* **3**: 200–231.
- Ruggiero, R.G. 1991. Hunting success of African Peregrine Falcons in the Central African Republic. *Gabari* **6**: 16–19.

- Tarboton, W.R.** 1984. Behaviour of the African Peregrine during incubation. *Raptor Res.* **18**: 131–136.
- Tarboton, W.R. & Allan, D.G.** 1984. The status and conservation of birds of prey in the Transvaal. *Transvaal Mus. Monogr.* **3**: 1–115.
- Temeles, E.J.** 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *Am. Nat.* **125**: 485–499.
- Thiollay, J.M.** 1988. Prey availability limiting an island population of Peregrine Falcons in Tunisia. In Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. (eds) *Peregrine Falcon Populations: their Management and Recovery*: 701–710. Idaho: The Peregrine Fund.
- Treleaven, R.B.** 1980. High and low intensity hunting in raptors. *Z. Tierpsychol.* **54**: 339–345.
- Tucker, V.A.** 1998. Gliding flight: speed and acceleration of ideal falcons during diving and pull out. *J. Exp. Biol.* **201**: 403–414.
- Zar, J.H.** 1984. *Biostatistical Analysis*. New York: Prentice-Hall.

Received 29 September 1998; revision accepted 30 March 1999

APPENDIX 1

Total sampling effort and 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	Total observation time (h)	Time observed (h)		No. of hunts (No. successful)		
		Males	Females	Males	Females	Pairs
Cape Peninsula						
PA1	618.9	264.6	371.3	130 (6)	574 (50)	52 (1)
PA2	686.7	258.5	421.4	114 (16)	121 (19)	32 (2)
PA3	206.4	55.9	62.3	20 (0)	13 (1)	17 (7)
PA4	80.2	3.8	14.0	0 (0)	3 (0)	0 (0)
PA6	62.5	11.5	21.4	1 (0)	3 (0)	0 (0)
PA7	104.5	23.1	36.5	2 (0)	3 (0)	0 (0)
PA8	229.7	84.5	101.4	9 (1)	21 (1)	4 (1)
PA13	86.3	18.3	26.3	4 (0)	6 (0)	2 (1)
Subtotal	2075.2	720.1	1054.5	280 (23)	744 (71)	107 (12)
Orange River						
PB1	53.8	9.8	21.4	0 (0)	7 (4)	1 (0)
PB2	70.6	18.7	34.3	3 (1)	6 (1)	0 (0)
PB3	179.0	101.2	119.5	75 (13)	36 (8)	12 (3)
PB4	92.7	36.0	43.5	10 (7)	13 (3)	5 (3)
Subtotal	396.1	165.7	218.6	88 (21)	62 (16)	18 (6)
Soutpansberg						
PC2	51.6	18.5	30.3	3 (1)	2 (0)	0 (0)
PC3	74.4	10.6	28.5	1 (0)	2 (0)	0 (0)
PC4	59.3	11.6	32.2	0 (0)	1 (0)	0 (0)
PC5	72.4	14.9	45.2	0 (0)	10 (0)	0 (0)
Subtotal	257.7	55.6	136.2	4 (1)	15 (0)	0 (0)

APPENDIX 2

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 close with it).
-