

HOME RANGE SIZE AND HABITAT REQUIREMENTS OF PEREGRINE FALCONS ON THE CAPE PENINSULA, SOUTH AFRICA

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ABSTRACT.—Two adult male and two adult female Peregrine Falcons (*Falco peregrinus*) were radiotracked in adjacent territories on the Cape Peninsula, South Africa between 1989–94. The falcons were tracked from two fixed stations over periods of 2–3 wk. The objective of the study was to determine the spatial and habitat requirements of peregrines and their ranging behavior. Males occupied larger home ranges than females, and females were more sedentary, spending over 50% of their time at the nest cliff. The home ranges of neighboring birds overlapped by about 20%, but neighbors tended not to forage in the same area on the same day. Areas with cliffs and ridges were preferred to slopes and flats, but other habitat and land-use categories were used randomly.

KEY WORDS: *peregrine falcon; Falco peregrinus; Cape Peninsula; home range; habitat use.*

Tamaño del rango de hogar y requerimientos de habitat de Halcón Peregrino en la Península del Cabo, Suráfrica.

RESUMEN.—Dos machos adultos y dos hembras adultas de Halcón Peregrino (*Falco peregrinus*) fueron estudiados mediante telemetría en territorios de la Península del Cabo, Suráfrica, entre 1989–94. El seguimiento fue hecho desde dos estaciones fijas por períodos de dos a tres semanas. El objetivo de este estudio era el determinar los requerimientos espaciales y de habitat de los Peregrinos y sus hábitos de forrajeo. Los machos ocuparon rangos de hogar mas grandes que las hembras, las hembras fueron mas sedentarias y emplearon el 50% del tiempo en el risco de anidación. Los rangos de hogar de los halcones vecinos se traslaparon en un 20%, pero tendían a no forrajear en las mismas áreas ni en los mismos días. Las áreas con riscos y acantilados fueron preferidas a las montañas y planicies, otras categorías de habitat y usos del suelo fueron utilizados al azar.

[Traducción de César Márquez]

Radiotracking of raptors can provide useful estimates of the extent and speed of their movements (Kenward 1987). We analyzed radiotelemetry data to investigate the ranging behavior of Peregrine Falcons (*Falco peregrinus*) on the Cape Peninsula, South Africa. Few studies have directly measured the extent and distribution of peregrine home ranges, and the spatial and habitat requirements of African peregrines (*F. p. minor*) are poorly known. The objectives of this study were to estimate the size of peregrine home ranges and the degree of overlap between neighboring territories, to estimate the frequency, speed and distance of falcon movements and to assess habitat use in relation to its availability. Because of practical constraints, we obtained only a moderate number of

reliable locations for a small sample of birds, and therefore adopted a conservative approach to the analysis and interpretation of our data.

METHODS

The study area was located in a central, discontinuous range of mountains and rocky ridges extending southward from Table Mountain on the Cape Peninsula (Fig. 1). The area has a mosaic of low-growing, heath-like fynbos vegetation types, interspersed with patches of forest and woodland. The suburbs of Cape Town extend along the east and west sides of Table Mountain and across the Cape Flats to the southeast. The east coast of the peninsula is built up along its northern half and the west coast features scattered settlements extending south to Scarborough. A band of suburban development connects Fish Hoek on the east coast with Noordhoek on the west. Altitude ranges from sea level to about 1100 m. Annual rainfall varies locally from about 40–200 cm, and falls mostly during winter (May–September) (Cowling et al. 1996). Temperature ranges from an average winter minimum of about 9°C to an average summer maximum of about 25°C.

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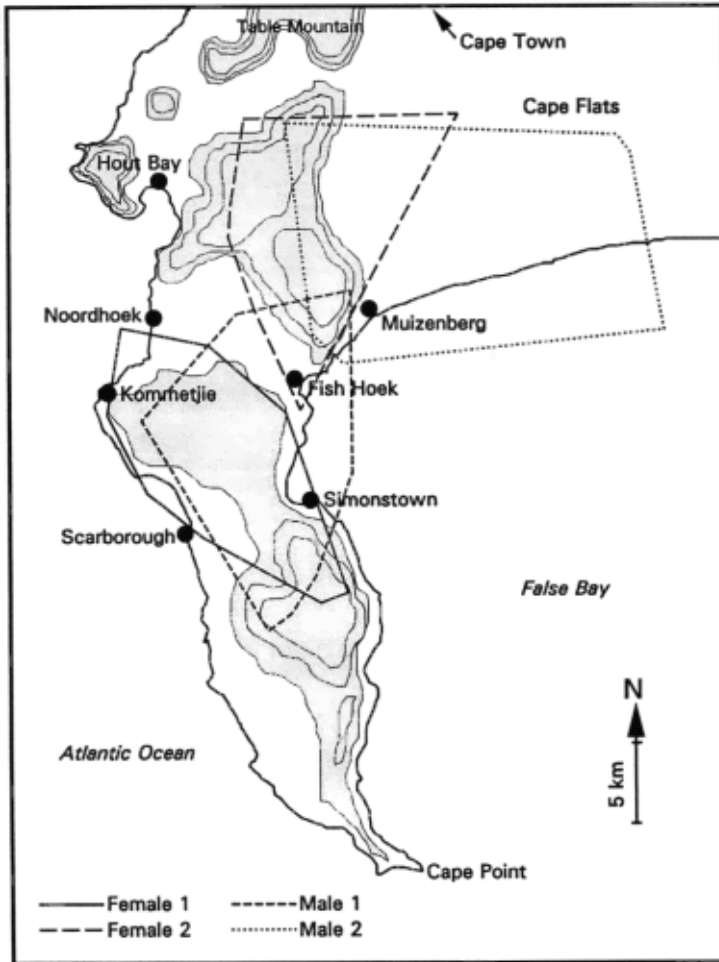


Figure 1. The Cape Peninsula south of Table Mountain, showing the home ranges (100% MCPs) of the four radio-tagged Peregrine Falcons in relation to the peninsula mountain chain and the main urban centers.

Four territorial adults were radiotracked during two study periods. Female 1 (F1) occupied a cliff on the southwest coast of the peninsula (Fig. 1) and was trapped and instrumented on 6 September 1989. This bird was tracked for 7 d between 21 September and 13 October for a total of 55.5 h. The earliest tracking began was at 0755 H and the latest it ended was at 1822 H. Female 2 (F2), male 1 (M1) and male 2 (M2) were from three separate but adjacent territories on the central eastern side of the peninsula. They were instrumented between 21 July–15 August 1994, and were tracked simultaneously on 9 days between 1–26 August for a total of 66.8 h. The earliest tracking of these birds began at 0700 H and the latest ended at 1830 H. M1 occupied a territory adjacent to F1 in 1994, but this territory was not occupied when F1 was tracked in 1989.

We attached the Biotrack transmitters (frequency range 150–151 MHz) with both main and ground plane

antennae using tail mounts (Kenward 1978), except that the attachment threads were sewn through the vane of a central rectrix on F1 only, and were tied around the vanes and sealed with epoxy on the other three birds. This was a precaution against feather damage and reduced the time and amount of manipulation required to fit each transmitter. Because they were larger, F1 and F2 were instrumented with heavier 12 g (1.3% body mass) and 7.5 g (0.9% body mass) transmitters, respectively, to obtain more power. These transmitters had an expected life of five and two months, respectively. Males were each instrumented with lighter transmitters (5 g, <1% of body mass) with an expected life of 10–14 d. All of the transmitters had nominal line-of-sight reception ranges of at least 20 km.

Tracking was carried out from two fixed stations, positioned at high points overlooking the territories. F1 was tracked from stations 4 km apart, and 2 km and 3.5 km

from the nest cliff (Fig. 1). F2 and the two males were tracked from stations 8 km apart, and 0.2 km and 11 km from each nest cliff. Locations of falcons were obtained using Yaesu FT-290R II transceivers and paired, in phase, five-element Yagi antennae, connected through a null-peak switch box to improve location accuracy (Kenward 1987). Directional fixes on each transmitter were taken synchronously from each station at prearranged intervals of 10–30 min. Bearings were recorded for each fix using a Recta DP 2 hand-held compass. Data from the two stations were combined later, and locations for each pair of fixes were plotted manually by triangulation on 1:50 000 topographic maps.

Fix bearing error (Lee et al. 1985) was measured at three of the four stations used by tracking a transmitter carried by car along a route through the study area not known by the observers at each station. Periodically, the car was stopped, the driver recorded the exact position and time, and held the transmitter as high as possible above the vehicle, turning it around to modulate the signal, simulating a moving bird. Observers at the tracking stations took fixes on the transmitter signal and recorded a time and compass bearing for each fix. Using this technique, bias and precision (Lee et al. 1985) at the three stations were calculated as $2.7^\circ \pm 2.2^\circ$ ($N = 9$ fixes), $4.1^\circ \pm 3.7^\circ$ ($N = 10$ fixes) and $2.4^\circ \pm 2.1^\circ$ ($N = 8$ fixes), with an overall bias of 3.1° for the study, which resulted in a location error of about 500 m over a tracking distance of 10 km. This figure may be higher than the actual bias incurred because the test transmitters were closer to the ground, and therefore more susceptible to signal bounce and interference than transmitters carried on prominently perched or flying birds.

We used the home range analysis program CALHOME (U.S. Forest Service, California Dept. of Fish and Game 1994) to determine the size and distribution of falcon home ranges. We converted our latitude-longitude locations to a metric format compatible with CALHOME using its associated utility program, LATLONG. Our location sample sizes were limited, so we used the nonpredictive minimum convex polygon method (Mohr 1947) to estimate range sizes. We produced 100% minimum convex polygon (MCP) home ranges for each bird for the entire study period and daily ranges for each tracking day with ≥ 6 hr of accumulated tracking time. Daily ranges were generated primarily to examine the frequency with which neighboring birds foraged in the same areas on the same day. The combined data for each bird were analyzed using the adaptive kernel method (Worton 1989) to illustrate patterns of home range use. Locational data were imported into the GIS ARC/INFO ver. 6.1.1 (Environmental Systems Research Institute, Redlands, California) to calculate the area of daily and home range overlap between the tracked birds.

Using ARC/INFO, we isolated the locations which placed each of the falcons at their respective nest cliffs. Time elapsed over each series of consecutive nest cliff locations was summed to derive an estimate of cliff attendance for each bird, expressed as a percentage of the time over which the bird was tracked. Each series of consecutive locations away from the nest cliff was considered to be an excursion or ranging flight. ARC/INFO facilitated the calculation of distances between successive lo-

cations allowing us to estimate the minimum distance covered by each falcon per hour of tracking time on each excursion away from its nest cliff and during the entire tracking period. Comparable average and maximum speed indices were calculated simply by dividing interlocation distance by interlocation interval for all cases where the interlocation distance exceeded zero and the interval between successive locations was 10–15 min.

We overlaid our telemetry data on previously compiled GIS coverages of the distribution of land use and vegetation (see Trinder-Smith et al. 1996 for descriptions of these databases) on the Cape Peninsula. These coverages were simplified into fewer, broader categories for our analysis by combining like habitats (e.g., five types of proteoid fynbos were considered as one habitat category). Using ARC/INFO, we calculated habitat availability (A) for each bird as the relative proportion of each habitat type present in its home range. In order to account for the level of bias affecting the accuracy of telemetry data, each location was buffered with a circle (diameter 500 m) and the area of each habitat within these buffers was calculated. Habitat use (U) was expressed as the total area of each habitat type contained within the total area of the buffered points.

Using information compiled by Forestek (CSIR 1995), a 500×500 m grid covering the Cape Peninsula was generated, containing information on the location of steep ridges and cliffs. A was measured in terms of the presence/absence of cliffs in the grid cells comprising each home range. U was determined as the proportion of each location which fell in cells with or without cliffs.

Ivlev's (1961) electivity index E , which provides a simple measure of "preference" or "avoidance," was calculated for each bird for each habitat type where $E = U - A/U + A$. Nonparametric Kruskal-Wallis (land use and vegetation) or Wilcoxon paired signed-rank (cliffs) tests (e.g., Kenward and Walls 1994) were used to determine whether patterns of habitat use differed significantly from random.

Peregrines generally spend fairly long periods of the day perched at their nest cliffs (Jenkins 1987, 1995). In order to examine habitat use by ranging or foraging birds more closely, the above analyses were repeated with the nest cliff locations for each individual excluded. Home ranges were also overlaid on a simplified coverage of land tenure and nature reserves on the Cape Peninsula (Cowling et al. 1996, Trinder-Smith et al. 1996), to determine the extent to which their spatial requirements are met by the existing or possible future reserve networks.

RESULTS

None of the transmitters malfunctioned; however, three of the four peregrines molted their rectrices prematurely shedding their transmitters. An additional male and female that were instrumented lost their transmitters within 11 d and were not tracked. F1 lost its transmitter after 40 d but before the completion of scheduled tracking. M1 and M2 molted their tail feathers after 31 and 88 d respectively, and F2 was recovered injured with its transmitter still attached and operating 56 d after it was

Table 1. Radiotelemetry data obtained for four Peregrine Falcons on the Cape Peninsula.

BIRD	DAYS		NUMBER OF LOCATIONS	AVERAGE
	TRACKED (+½ DAYS)	HOURS TRACKED		LOCATION INTERVAL (MIN)
Female 1	5 (+2)	54.4	307	10.6
Female 2	5 (+4)	63.1	161	23.5
Male 1	4 (+5)	62.3	153	24.4
Male 2	6 (+1)	57.7	115	30.1
Overall	20 (+12)	237.5	736	22.2

instrumented. The two untracked birds which shed their transmitters quickly and M1 did not grow new central rectrices during molt in the subsequent season suggesting that the transmitters may have caused damage to the feather follicles.

On average, only 59% of the locations recorded at each of the tracking stations were acceptable. In 9% of cases, signal distortion or observer error produced divergent fix pairs which could not be triangulated. Thirty-two percent of locations were unpaired because of signal interruption at one of the two tracking stations.

We were able, however, to compile about 20 d (240 h) of telemetry data describing the movements of the four peregrines we tracked (Table 1). Range size and habitat use of each individual were assessed in terms of the distribution of at least 100 locations, with an average interlocation interval of about 22 min.

The two females occupied smaller home ranges than the two males, although the average daily ranges of the four birds were similar in size (Table 2). Home range areas calculated using the adaptive

kernel method showed the relatively sedentary nature of the peregrines, with up to 95% of the locations sufficiently densely packed to account for only about 30% of the total home range predicted for each falcon. Each of the home ranges of the three peregrines tracked in 1994 overlapped substantially with at least one other falcon (Fig. 1). F2 shared an area of 15.2 km² with M1 and 52.6 km² with M2. The home ranges of the two males overlapped by 6.1 km². There was less overlap in the daily ranges, with F2 overlapping on 1 d with M1 by 2.7 km², and on 3 d with M2 by <1–2.3 km². The daily ranges of the two males did not overlap.

The female peregrines spent over half of the tracking time at their respective nest cliffs (F1 = 54%, F2 = 53%), whereas the two males were at their nest cliffs for only about 20% of the total tracking time (M1 = 15%, M2 = 29%). Nearly 80 excursions from the nest cliff were recorded (Table 3). These ranging flights were between <1 km and >80 km in length (Table 3). Males moved less frequently but covered longer distances (Fig. 2). Over the entire tracking period F1 covered a minimum total distance of 268 km and ranged up to 9.2 km from its nest cliff, and F2 covered 228 km and flew up to 9.2 km from its nest cliff; M1 covered 350 km and ranged out to 11.1 km, while M2 covered 346 km and ranged out to 16.4 km. Males also flew farther per tracking hour than females, and achieved higher maximum speeds between consecutive locations (Table 3).

F2 and M2 occupied territories in the northern half of the peninsula (Fig. 1). They frequently flew out over the Cape Flats so their home ranges included tracts of urban and suburban land, and featured asteracious fynbos, the dominant natural vegetation in these low relief, coastal areas (Table 4).

Table 2. Estimates of home range size and average daily range size (100% MCPs) for four Peregrine Falcons on the Cape Peninsula based on telemetry data, with additional home range size estimates calculated using the adaptive kernel method for the densest percentage of the locations obtained for each bird. Daily ranges were generated from 34–67 locations for F1, 12–27 locations for F2, 19–25 locations for M1 and 9–24 locations for M2.

BIRD	HOME RANGE (km ²)	AVERAGE DAILY RANGE (km ²)	ADAPTIVE KERNEL (km ²)			
			50%	75%	95%	100%
Female 1	89.7	25.9	0.2	4.0	52.6	172.2
Female 2	94.7	20.2	0.1	9.8	67.7	269.2
Male 1	115.2	22.8	4.5	21.1	84.7	159.2
Male 2	192.1	22.3	13.8	37.6	140.4	419.4
Average	123.0	22.8	4.7	18.1	86.3	255.0

Table 3. Number of excursions or ranging flights away from nest cliffs, average excursion distance, average distance covered per hour of tracking time, and maximum speed between consecutive locations recorded for four Peregrine Falcons radiotracked on the Cape Peninsula.

BIRD	NUMBER OF EXCURSIONS	AVERAGE DISTANCE (km)	AVERAGE km PER TRACKING HOUR	MAXIMUM SPEED (km/h)
Female 1	26	10.3 (0.2–43.5)	5.1	40.7
Female 2	18	12.7 (1.4–49.6)	4.1	44.5
Male 1	16	21.9 (0.6–83.5)	6.1	59.4
Male 2	16	21.7 (0.5–75.0)	6.7	63.0
Overall	76	16.7 (0.2–83.5)	5.5	51.9

F1 and M1 occupied territories farther south on the peninsula, and ranged over largely unused land, covered mostly by proteoid fynbos. Hence, the habitat composition of each of the home ranges seemed to be largely dependent on the location of the territory. There were no consistent patterns in the habitat electivity indices of the four birds (Table 5). This suggested that habitat use, defined in terms of land use (including nest cliff locations, Kruskal-Wallis $H = 4.46$, $P = 0.35$, excluding nest cliff locations, $H = 4.16$, $P = 0.38$) or vegetation (including nest cliff locations, $H = 7.82$, $P = 0.35$, excluding nest cliff locations, $H = 5.78$, $P = 0.57$) was random. However, when habitat use was defined by topography, peregrines on the Cape Peninsula significantly favored cliffs and ridges over slopes and flats (Table 5, Wilcoxon signed-rank test, $P = 0.045$, for electivity indices both including and excluding nest cliff locations).

About 45% (range = 33–57%) of each of the

four peregrine home ranges fell within state-owned land, managed by the Western Cape Provincial Administration or by local municipalities. The remaining 55% is privately owned. On average, about 11% of each of the four home ranges was within the existing reserve network of the peninsula (F1 = 3%, F2 = 26%, M1 = 12%, M2 = 4%).

DISCUSSION

The transmitters we used in this study were considerably lighter than the recommended upper limit of 3% of body mass (Kenward 1987), and each was attached carefully and with as little manipulation of the tail feathers as possible. Despite this, five of six birds shed their transmitters prematurely. We suspect that the bulk or shape of the transmitters, rather than their mass, caused this high incidence of premature molting. In particular, the ground plane antenna of each transmitter protruded above the otherwise streamlined profile

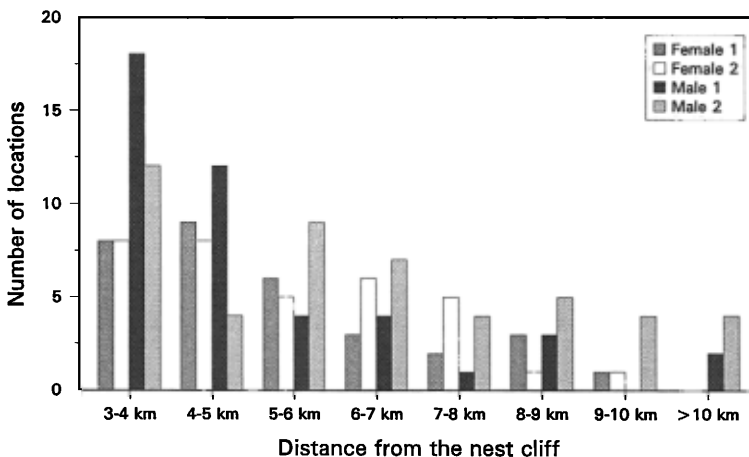


Figure 2. The number of locations recorded for a range of distance intervals away from the nest cliff for each of the four Peregrine Falcons radiotracked on the Cape Peninsula.

Table 4. Habitat composition of the home ranges of four Peregrine Falcons radiotracked on the Cape Peninsula.

HABITAT CATEGORY	FEMALE 1		FEMALE 2		MALE 1		MALE 2	
	AREA ¹	% ²	AREA	%	AREA	%	AREA	%
Land use								
Waterbodies	8.0	9.0	1.9	2.0	20.8	18.0	63.0	32.8
Unused vegetated	75.6	84.2	24.0	25.3	81.7	70.9	56.9	29.6
Unused open	0.4	0.5	18.3	19.3	0.8	0.7	20.6	10.7
Suburban	3.2	3.6	26.8	28.2	6.3	5.5	28.2	14.7
Urban	2.5	2.7	23.9	25.2	5.7	5.0	23.3	12.1
Vegetation								
Restioid fynbos	0.6	0.7	0.0	0.0	2.7	2.3	0.0	0.0
Asteracious fynbos	4.6	5.1	63.9	67.4	7.1	6.2	121.2	63.1
Ericacious fynbos	1.0	1.1	0.0	0.0	0.1	0.1	0.0	0.0
Proteoid fynbos	72.0	80.3	29.1	30.7	83.0	72.0	7.6	4.0
Cliff communities	0.3	0.3	0.1	0.1	0.1	0.1	0.0	0.0
Forest and thicket	0.4	0.5	0.5	0.5	0.2	0.2	0.2	0.1
Wetlands	1.5	1.7	1.3	1.4	0.7	0.6	8.3	4.3
Open sea	9.3	10.4	0.0	0.0	21.4	18.6	54.7	28.5

¹ km².

² % of home range area.

Table 5. Ivlev's electivity indices describing habitat utilization by four Peregrine Falcons on the Cape Peninsula, based on the distribution of radiotelemetry locations.

CATEGORY	FEMALE 1	FEMALE 2	MALE 1	MALE 2
Land use excluding nest cliff locations				
Waterbodies	-0.62	-0.54	0.18	-0.51
Unused vegetated	0.06	0.30	-0.20	0.04
Unused open	-0.67	-0.02	0.36	-0.26
Suburban	-0.47	-0.26	0.41	0.20
Urban	-0.42	-0.24	0.42	0.26
Vegetation excluding nest cliff locations				
Restioid fynbos	0.12	na	-0.48	na
Asteracious fynbos	-0.59	-0.24	0.56	-0.01
Ericacious fynbos	-0.37	na	0.60	na
Proteoid fynbos	0.07	0.31	-0.21	0.75
Cliff communities	0.68	0.50	0.00	na
Forest and thicket	-0.11	-1.00	-1.00	0.88
Wetlands	-0.26	-0.40	0.33	0.00
Open sea	-0.72	na	0.20	-0.71
Topography including nest cliff locations				
Cliffs and ridges	0.73	0.61	0.64	0.85
Slopes and flats	-0.16	-0.16	-0.13	-0.15
Topography excluding nest cliff locations				
Cliffs and ridges	0.75	0.42	0.32	0.70
Slopes and flats	-0.17	-0.07	-0.03	-0.05

of the flying bird, and may have caused sufficient turbulence during high speed maneuvers to destabilize and ultimately dislodge the rectrix.

Activities of each of the peregrines were centered on nest cliffs, and only a small number of distant locations accounted for most of their home ranges. Sample sizes (tracking time, number of locations) may not have been sufficient to adequately represent these irregular movements causing us to underestimate the actual size of the home ranges. Nevertheless, our home range estimates were similar to those recorded for peregrines in previous studies (e.g., Mearns 1985, White and Nelson 1991).

The Cape Peninsula mountain chain (and its adjacent coastal flats) occupies an area of about 440 km² and supports at least 12 pairs of Peregrine Falcons. If these resident pairs maintained exclusive home ranges, each range would comprise about 37 km². Telemetry data suggest that peninsula peregrines require over three times this area, and that the home ranges of adjacent pairs overlap by about 20%. A study of urban-breeding Merlins (*F. columbarius*) recorded a similar degree of overlap between neighboring territories (Sohdi and Oliphant 1992). It may be significant that the daily ranges of peninsula peregrines overlapped less than their aggregate home ranges, suggesting that falcons from different territories tended not to forage over the same area at the same time.

Although only two birds of each sex were tracked, differences in the ranging behavior of males and females were evident. Tracking took place immediately before the onset of breeding and each of the instrumented peregrines and their mates had commenced nuptial displays, copulation, and courtship feeding. Hence, the males ranged more extensively and covered ground more rapidly in order to provide food for their females, whereas females were relatively sedentary (e.g., Newton 1979, Ratcliffe 1993). More comprehensive estimates of the foraging ranges of the females could have been obtained by tracking them much later in the breeding season or in the nonbreeding season (Enderson and Kirven 1983, Mearns 1985, Kimsey and Marzluff 1993).

Our average maximum speeds (41–52 km/h) were similar to predicted (56 km/h) and observed (46 km/h) cruising speeds of African peregrines (Jenkins 1995), and probably represent occasions when peregrines traveled most directly between consecutive locations.

The absence of significant land-use or vegetation preferences by these peregrines may indicate that the scale, accuracy or number of telemetry locations obtained were inadequate to show preferences. Certainly, foraging conditions for peregrines are likely to vary in the different habitat categories we defined and we expected differential habitat use as a result. However, the relative importance of habitats as sources of prey may not be reflected in the distribution of the locations. Peregrines generally hunt from perched or aerial vantage points and make rapid strikes at flying prey (usually birds), often over long distances (Cade 1982). While hunts may be concluded over particular habitats where prey are numerous or vulnerable to predation, falcons do not necessarily make very frequent visits to these foraging areas, or spend long periods of time in them. Cliffs and ridges were used extensively, probably because they provided elevated sites for perch hunting, and updrafts which facilitate aerial hunting and cross-country flying (Jenkins 1995).

The Cape Peninsula is bounded by the city of Cape Town and its extensive suburbs, but much of the mountain chain south of the urban center remains undeveloped and comprises a loosely-connected network of conservation areas. While the peninsula generally lacks significant populations of local endemic bird species (Hockey et al. 1989, Cowling et al. 1996, Picker and Samways 1996), it supports one of the densest peregrine populations recorded in sub-Saharan Africa (average nearest neighbor distance = 4.6 km, range 1.3–7.8 km, unpubl. data). Nine of the peregrine nest sites we know of on the peninsula are in existing nature reserves and two of the remaining three sites are located within the Cape Peninsula Protected Natural Environment (CPPNE) (Cowling et al. 1996), which is likely to be incorporated into any extension of the area's present reserve system (Trinder-Smith et al. 1996, van Niekerk 1996). However, the individuals tracked during this study ranged extensively beyond the CPPNE boundary, over nonconserved and privately-owned land that is unlikely to be conserved in the future (Trinder-Smith et al. 1996). Much of this land has already been developed. Thus, while the nest sites and preferred habitats (cliffs and ridges) of peregrines on the peninsula are likely to be preserved, the spatial and habitat requirements of most pairs are not met by existing or possible future conservation areas. Our analysis of habitat use suggests that the spread of

urban development into presently undeveloped areas of peregrine home ranges may not be detrimental, and peregrines may benefit from the abundance of prey associated with the metropolitan area fringing the mountains. However, their capacity to exploit this food base may depend on the nature of the urban environment. For example, peregrines frequently use tall trees or buildings as feeding or hunting perches when foraging in suburban areas. Such vantage points are not a feature of low-cost housing schemes, which are currently the dominant form of urbanization on the peninsula. Hence, the value of certain areas to foraging falcons may decline with the future spread of development.

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