BEHAVIOR OF THE AFRICAN PEREGRINE DURING INCUBATION

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ABSTRACT - Dawn-to-dusk watches were made during 5 d at a Peregrine Falcon (*Falco peregrinus*) nest with eggs in the Transvaal and all activity was recorded. The male incubated 35% of the day and the female 65%. Their incubation shifts averaged, respectively, 1 h 30 min and 2 h 25 min. Eggs were covered for 98% of the day. The female slept on the nest at night. The non-incubating bird was absent from the nest-cliff for periods averaging 2 h at a time and totalling about 3 h each day. It may have hunted during this time. Hunting by chasing and 'flushing' is described. Twenty-one prey items from 3 eyries were all birds, especially pigeons and doves (46%). The high share of the incubation done by the male, the abnormal hunting by the female during incubation, and the apparent rarity of Peregrines in the Transvaal are discussed.

The status of the African race of the Peregrine Falcon (*Falco peregrinus minor*)is poorly documented, though it appears to be scarce and very localized throughout its range (Cade 1969; MacWorth-Praed and Grant 1957, 1962; Snow 1978). It is described as being a rare breeding resident and possibly threatened in South Africa (Siegfried et al. 1976). During a 3-yr survey of falconiforms in the Transvaal only 10 breeding pairs were located in 286,300 km^2 (Tarboton and Allan 1984). Data herein may give insight into the factors contributing to its rarity in South Africa, and may provide useful comparative data for similar studies being done on the Lanner Falcon (*Falco biarmicus*) (Kemp, *in prep*).

Detailed observations were made during 5 d at an eyrie in the eastern Transvaal Escarpment Region (Site 1). This paper describes observed breeding and hunting behavior of this pair and includes observations made at 2 other eyries (Sites 2 and 3). Obviously the behavior of a single pair may not represent the species as a whole; in the absence of other published data on the biology of the African Peregrine, these observations are given.

STUDY AREA AND METHODS

The peregrine pair at Site 1 laid eggs in 1979 on an old nest probably built by the Black Stork (*Ciconia nigra*) on a ledge 40 m from the base of a 140 m east-facing cliff overlooking a long, sloping valley extensively planted under pines and eucalyptus. When first located in May 1979 a single male peregrine was seen at the nest-cliff. Observations were made between 5-11 September when the site was occupied by a pair incubating 3 eggs. On 2 November the pair was accompanied by 2 just-fledged young. Both male and female were adult and they could be distinguished by their size difference and the male's noticeably brighter-yellow eye ring, cere and feet.

The nest-cliff was observed continuously from dawn to dusk for 5 d (5-8 and 11 September) totaling 61 h with an additional 2 h 5 min on 10 September. Three observers watched in rotation from a vantage point on the slope directly below the nest. Two tripod-mounted telescopes were used, one trained on the nest and the other following the movements of the non-incubating bird. All activity, including nest change-overs, agonistic behavior, activities while perched (e.g. preening), vocalizations, and flights were recorded. During periods of rapid action a cassette recorder was used to record activity.

Local sunrise and sunset at the site were, respectively, 0600 H and about 1745 H during the observation period, but it became too dark for observations after 1800 H and before 1530 H. The nest was shaded after 1330 H and the nest-cliff after 1550 H. During 3 d weather was cloudless and warm with little or no wind, and on 2 d it was cold, overcast and windy. No behavioral difference by the birds on clear and overcast days were noticed.

RESULTS

Eggs were incubated for 97.9% of the daytime (n = 61 h); on 4 d this averaged 99.3%, whereas on 1 d the eggs were covered for only 92.2% of the time. Both sexes incubated during daytime, but only the female spent the night on the nest (n = 5). Overall the female did the greater share of incubation, although on 1 d the male's exceeded the female's. The respective proportion of incubation ($\bar{x}$/s.d.;range) during 5 d was, for the male: 34.7/17.5; 11.6-59.5, and for the female: 65.3/17.5; 40.5-83.4. If the female's overnight incubating is included, the respective male:female proportion of the incubation is 17.7:82.3.

Daytime incubating shifts by the female averaged 2 h 25 min (s.d. = 1 h 6 min, range = 29 min - 4 h 3 min, n = 11) and those of the male averaged 1 h 30 min. (s.d. = 1 h 17 min, range = 8 min - 4 h 14 min, n = 14) (the difference is not significant). The male had both the longest and shortest daytime incubating shifts (respectively, 4 h 14 min and 8 min), although if the female's overnight shifts are included, these would exceed the longest shifts by the male. Her longest continuous incubation shift in this case was 15 h 52 min.

Most observed nest change-overs (n = 27) were similar in that the relieving bird flew unannounced to the nest and alighted beside the incubating bird. One or both birds then uttered a series of *'tjak-ak'*

Table 1. Total time during 5 d, given in min and as a percentage, in which the non-incubating bird was present at, and absent from, the nest-cliff.

WHEREABOUTS OF NON-INCUBATING BIRD	TIME (MIN)		%	
	MALE	FEMALE	MALE	FEMALE
Present at nest-cliff	562	735	42.0	30.7
Absent from nest-cliff	777	1637	58.0	68.3
Unknown	0	26		1.0
Totals	1339	2398	100.0	100.0

notes before the incubating bird flew off and the relieving bird incubated. Occasionally other vocalizations (e.g. whining *'weee-e-k'*) were used at change-overs. The male often (10/15 times) appeared to be reluctant to give up incubating when relieved by the female. On such occasions one or both birds called much longer than usual, uttering 25-30 *'tjak-ak'* notes. Invariably the female supplanted the male in these instances, whereas the male frequently ($n = 10$) came to the nest to relieve the incubating female but was unable to dislodge her. Occasionally ($n = 3$) the female had already left the nest when the male arrived to incubate and he took over silently.

There was no regular pattern of shifts by sex during the 5 d, apart from the first and last shift each day by the female. The male relieved her before sunrise (averaging 28 min before sunrise) on 4 of the 5 d. The female's last shift continued overnight and commenced at various times between 47 min - 3 h 59 min before sunset ($\bar{X}$ = 1 h 54 min).

Activity of the Non-incubating Bird — Often the non-incubating bird left the vicinity of the nest-cliff, presumably to hunt since both birds returned after absences with bulging crops. When not incubating, the male was absent a significantly greater proportion of the time than the female ($P < 0.0001$, see Table 1). On average, the non-incubating bird was absent from the nest-cliff for about two-thirds of each day ($\bar{X}$/s.d. = 8 h 3 min/1 h 35 min; range = 5 h 17 min - 9 h 7 min, $n = 5$). The incubating bird was alone at the nest-cliff for 71% of the day (female) or 62% of the day (male).

The Crowned Eagle (*Spizaetus coronatus*), Jackal Buzzard (*Buteo rufofuscus*), Gymnogene (*Polyboroides radiatus*) and the White-necked Raven (*Corvus albicollis*) were invariably chased and harrassed by the non-incubating bird if they passed the nest-cliff when he or she was present. The incubating bird was never seen to leave the nest and assist its mate during these pursuits, nor did it attempt to chase off passing birds of prey when the mate was absent. On 1 occasion the nest-cliff and eggs were left entirely unattended for 55 min when the female left the nest to pursue, catch and eat a passing pigeon (see *Hunting Behavior*). Black Storks, which came and went continuously from an active nest about 500 m away on the cliff were not molested.

Typically both birds, at the end of an incubating shift, flew to a favored perch, defecated, and commenced preening, and later started other maintenance activities such as stretching, scratching or (occasionally) casting a pellet. On average, male and female spent, respectively 86 and 90 min/day (s.d. = 29 and 39 min respectively) actively preening on a perch (about 12% of each day). After a period of preening they usually became alert, looking about, making perch-changes or 'flush-hunting' (see *Hunting Behavior*) before taking flight, soaring high, and going out of view behind the nest-cliff.

Hunting Behavior — Most hunting and eating of prey apparently occurred away from the nest-cliff since only 2 successful prey strikes were observed in 5 d. In one of these the female left the nest to catch a passing pigeon which it ate away from the nest-cliff. In the other instance the male caught a small bird which it took back to the nest-cliff to eat. There was little prey pluckings below favored perches, and none at the nest, suggesting that during incubation prey was not frequently brought back to the nest-cliff to eat. During 5 d the male never brought food to offer the female and she appeared to provision herself entirely. In the instance where the male returned to the nest-cliff to eat prey, the female left the nest and attempted to take the remains from him after he had eaten for 10 min. They grappled for the prey on the male's perch before it fell and was lost in the forest below.

In addition to 2 successful strikes, 5 unsuccessful chases (2 by female, 3 by male) and 1 probably successful strike (female) were initiated from the nest-cliff. Three of these 8 attempts (all by the female) involved chasing birds, twice pigeons, which were flying past at least 2-3 km distant. In one case she soared briefly to gain height before attacking passing birds, flying with rapid wingbeats to a point ahead of the birds so as to intercept them. In one unsuccessful chase the 2 pursued pigeons changed direction as she approached, then dived downwards. She stooped unsuccessfully at them 3 times before they reached shelter in trees. In a second apparently successful chase the female's flight from take-off to strike lasted 120 ± 5 sec. It followed the same pattern in which the prey attempted to evade the peregrine by diving and the female spiralled down after it.

At site 2 a male stooped at and caught a swift (probably *Apus melba*) which was one of a large flock

Table 2. Peregrine prey recorded at 3 Transvaal eyries. Sites 1 and 2 are in the Escarpment Region, Sites 3 is in the Lowveld.

SOURCE OF DATA	PREY SPECIES	NO.
1. Prey remains found below perches on nest-cliffs;		
Site 1	Domestic Pigeon, *Columba livia*	4
	Red-eyed Dove, *Streptopelia semitorquata*	1
	Laughing Dove, *Streptopelia senegalensis*	1
	Cuckoo, *Chrysococcyx* sp.	1
Site 3	Red-eyed Dove *Streptopelia semitorquata*	1
	Green Pigeon, *Treron australis*	1
	Burchell's Coucal, *Centropus superciliousus*	1
	Swift, *Apus* sp.	1
	Red-faced Mousebird, *Colius indicus*	1
	Lilabreasted Roller, *Coracias caudata*	1
	African Hoopoe, *Upupa epops*	1
	Rock Martin, *Hirundo fuligula*	1
	Blackheaded Oriole, *Oriolus larvatus*	1
	Starling, *Lamprotornis* sp.	1
	Small passerine	1
2. Prey observed being caught		
Site 1	Domestic pigeon, *Columba livia*	1
	Small bird	1
Site 2	Swift, probably *Apus melba*	1
3. Unsuccessful prey strikes		
Site 1	Rock Pigeon, *Columba guinea*	1
	Pigeon, *Columba* sp.	2
	Redwinged Starling, *Onychognathus morio*	1
	Small bird	2
Site 2	Rock Pigeon, *Columba guinea*	1

spiralling around in the valley below the nest-cliff. The stoop lasted about 10 sec. The bird covered about 1 km and dropped about 300 m during the strike. It took the swift in its feet as it passed through the flock.

In a second hunting method peregrines attempted to flush prey ('flush-hunting') from the nest-cliff and then pursue it. Both male and female frequently did this, though never successfully. In 'flush-hunting' the peregrine changed its perch on the cliff frequently, doing small aerial circuits before re-alighting, sometimes flying up into small crevasses, clinging there briefly, and flying out again. Flushed birds which were unsuccessfully chased included a Rock Pigeon (*Columba guinea*), Redwinged Starling (*Onychognathus morio*) and two smaller birds. 'Flush-hunting' was also observed being used by the female peregrine at Site 2. In this case she flushed, but failed to catch, a Rock Pigeon. This method was frequently used by immature peregrines in the Aleutian Islands, Alaska, and by adults in Argentina (C.M. White, pers. comm.).

The non-incubating bird's frequent absences from the nest-cliff may have been for the purpose of hunting. These absences lasted, on average, about 2 h (respectively, $\bar{x}$/s.d.; range, for male: 2 h 8 min/55 min; 1 h - 3 h 40 min; n = 9, and female: 1 h 50 min/1 h 30 min; 33 min - 4 h 1 min; n = 7). On at least 2 occasions returning birds had bulging crops.

Prey — Prey data from 3 Transvaal peregrine eyries are given in Table 2. These include items identified from plucking found below perches on the nest-cliffs (18), prey observed being caught (3) and potential prey unsuccessfully chased (7). In all cases prey was avian, and in the wt.-range 25-300 g. Thirteen (46%) were pigeons and doves. The sample from Site 3, a low veld eyrie, includes several bird-species which are absent from the escarpment region.

DISCUSSION

Of special interest was the high proportion of incubation done by the male (35%) and independence of the female in obtaining food during incubation. This compares with the findings of Hustler (1983) in Zimbabwe. In some peregrine populations (e.g. in Alaska, Enderson *et al.* 1972) males may share up to a third of the incubation, but it is usual for females to take the major share (Cramp 1980). The independent hunting by the female at Site 1 is exceptional, since other studies indicate that she is provided with most or all of her food by the male during incubation (Brown and Amadon 1968; Cramp 1980). It would be instructive to determine whether these observations reflect an isolated occurence or occur generally in populations of *F.p. minor*.

These two features are at variance with a general pattern in falconiforms where reversed size dimorphism is closely correlated with rapaciousness, a difference in prey size taken by the sexes and often with the nature of parental roles (Selander 1966; Reynolds 1972; Amadon 1975). Thus bird-catching hawks which are the most rapacious tend to have the greatest size dimorphism, take prey in 2 size-classes according to sex and, during breeding, partition parental duties such that the female does most of the incubation while the male does most or all of the provisioning (Newton 1979). Peregrines have a large size dimorphism and are highly rapacious, yet the observations recorded here do not conform to the predicted model of partitioned parental roles. The behavior of the pair at Site 1 may have been atypical.

The rarity of the peregrine in the Transvaal (and elsewhere in southern Africa) has not yet been adequately accounted for. The Lanner Falcon, by contrast, is a relatively common bird (McLachlan and Liversidge 1978). A measure of the relative abundance of the two species in the Transvaal is shown by the number of breeding sites of each recorded during the survey of birds of prey during 1975-1981 when 14 peregrine and 151 lanner eyries were located (Tarboton and Allan 1984). I believe that indirect competition between the two species is partly responsible for the peregrine's rarity, and that the following contribute to this situation:

(1) Prey — Whereas peregrines take almost exclusively avian prey, lanners, that prey largely on birds, also take a variety of non-avian prey, including rodents, bats, lizards and locusts (Brown and Amadon 1968; Cramp 1980, pers. obs.).

(2) Hunting Methods — The peregrine is a specialized hunter, securing avian prey in the air by stooping on it at great speed, and it requires sufficient air-space in order to chase and catch its prey. The lanner often hunts by stooping, but also hunts from perches and frequently chases avian prey in level flight, pursues prey flushed by vehicles, animals or persons on foot, and snatches prey such as

young gamebirds and poultry from the ground (Brown and Amadon 1968; Cramp 1980, pers. obs.).

(3) Nest-sites — All 14 Transvaal peregrine eyries were on high cliffs (mean height 187 m), only one being on a cliff lower than 140 m. Most recorded lanner nest-sites in the Transvaal (n = 175) were similarly on cliffs (57%), but mainly on small cliffs (45%) less than 60 m in height. Many were also in crow nests on pylons (25%), on crow or eagle nests in trees (14%), and on buildings or in quarries (4%).

Lanners, with a broad feeding niche, may outperform peregrines (on an energy/time-cost basis) in some situations, while in other situations the opposite will occur. During breeding, when food demands are greatest, this difference between the two species will reflect their choice of breeding sites and their reproductive output. It is predicted that optimal breeding sites for peregrines will be on high cliffs overlooking airspace through which there is a steady passage of high-flying birds within striking range. In such situations a breeding pair can search for prey while perched on the nest-cliff and simultaneously be able to defend the nest from predators. Lanners, less specialized in making high-speed, long-range stoops, may not match the performance of peregrines breeding in such circumstances. However, on progressively lower cliffs (which offer peregrines a less effective striking height) or in situations where there is less prey passing within range of the cliffs, breeding sites become marginal for peregrines, and a threshhold would be reached where lanners, with their wider prey range and more diverse means of taking prey, outperform peregrines.

Peregrines breeding at marginal sites may incur higher energy costs than those breeding at optimal sites; both hunting away from the nest-cliff (necessitating frequent climbing in order to make stoops) and transporting food back to the nest, may be more time and energy consuming. Such disadvantages could leave nests exposed to potential predators and may result in a reduced provisioning rate, affecting reproductive performance negatively. The site observed may have been marginal since most hunting was done away from the cliff, and once during the 5-day watch the cliff was left entirely unattended for 55 min. This may also be why the female hunted for herself during incubation.

Elsewhere in the world the peregrine's preference for high cliffs has been noted (Hickey 1942; Ratcliffe 1962); and during the extirpation of *F. p. anatum* from northeastern America through pesticide contamination in the 1950's it was noted that the first eyries to be deserted were those on low cliffs, and the last to go were those on the highest cliffs (Hickey 1969). This supports the hypothesis that occupation of high cliffs has energy/time-cost benefits for peregrines breeding there. In areas where lanners (or other *Falco* species filling the 'lanner-niche') are absent, peregrines may occupy a wider range of breeding sites than otherwise, although the reproductive performance of pairs at marginal sites may not match that of pairs at optimal sites. Where lanners occur in sympatry, peregrines are excluded from many marginal sites by lanners because of the latter's more generalized hunting capabilities and efficiency at low sites.

Thus it is hypothesized that the rarity of peregrines in the Transvaal is the result of (1) the general scarcity of optimal breeding sites (i.e. high cliffs overlooking airspace offering sufficient prey-capture opportunities), and (2) the presence of lanners which outcompete them (on an energy/time-cost basis) and exclude them from marginal sites. Lanners are generally much more common, since by far the greater part of the Transvaal is a plateau with little or no relief. However, in parts of the Transvaal Escarpment Region where conditions favor peregrines, lanners are outnumbered by them. In one such area 4 peregrine eyries are known, compared with only 2 of lanners.

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LITERATURE CITED

Amadon, D. 1975. Why are female birds of prey larger than males? *Raptor Research* 9:1-11.

BROWN, L.H. AND D. AMADON. 1968. Eagles, hawks and falcons of the world, Vol. 2. Feltham: Country Life.

CADE, T.J. 1969. The status of the Peregrine and other Falconiformes in Africa, pp 289-321, in Hickey, J.J. (ed) Peregrine Falcon populations, their biology and decline. Madison: Univ. Wisc. Press.

CRAMP, S. 1980. Handbook of the birds of Europe, the Middle East and North Africa, Vol. 2. Oxford: Oxford Univ. Press.

Enderson, J.H., S.A. Temple and L.G. Swartz. 1972. Time-lapse photographic records of nesting Peregrine Falcons. *Living Bird* 11:113-128.

Herbert, R.A. and K.G.S. Herbert. 1965. Behaviour of Peregrine Falcons in the New York City Region. *Auk* 82:62-94.

Hickey, J.J. 1942. Eastern populations of the Duck Hawk. *Auk* 59:176-204.

Hickey, J.J. (ed). 1969. Peregrine Falcon populations, their biology and decline. Madison: Univ. Wisc. Press.

Hustler, K. 1983. Breeding biology of peregrine falcon in Zimbabwe. *Ostrich* 54: 161-171.

McLachlan, G.R. and R. Liversidge. 1978. Roberts' birds of South Africa, 4th ed. John Voelcker Bird Book Fund: Cape Town.

Macworth-Praed, D.W. and C.H.B. Grant. 1957. Birds of eastern and northeastern Africa, Ser. 1, Vol. 1. London: Longmans.

Macworth-Praed, C.W. and C.H.B. Grant. 1962. Birds of the southern third of Africa, Ser. 2, Vol. 1. London: Longmans.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, South Dakota.

Ratcliffe, D.A. 1962. Breeding density of the Peregrine *Falco peregrinus* and Raven *Corvus corax*. *Ibis* 104:13-39.

Reynolds, R.T. 1972. Sexual dimorphism in the accipiter hawks: a new hypothesis. *Condor* 74: 191-197.

Selander, R.K. 1966. Sexual dimorphism and the differential niche utilization in birds. *Condor* 68:113-151.

Siegfried, W.R., P.G.H. Forst, J. Cooper, and A.C. Kemp. 1976. South African Red Data Book: Aves. *S. Afr. National Sci. Prog. Rep.* 7. Pretoria: CSIR.

Snow, D.W. (ed). 1978. An atlas of speciation in African non-passerine birds. London: Trustees Brit. Mus. (Nat. Hist.).

Tarboton, W.R. and D.G. Allan. 1984. A survey of birds of prey in the Transvaal. Tvl. Mus. Monogr. No. 3.

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