The influence of nestling predation on nest site selection and behaviour of the bateleur

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Received 25 August 1987; accepted 15 January 1988

Appropriate nest site selection and the response of parents and nestlings to intruders near the nest, are behaviours that could be adaptive in a species that is prone to nestling predation. This study showed that predation of bateleur nestlings in the Kruger National Park was high, that behaviour of adults and nestlings towards intruders near the nest served to reduce the detectability of the nestling, and that bateleurs appeared to select nest sites for concealment and protection of the nestling. It is suggested that the high vulnerability of bateleur nestlings to predation is a consequence of the species' unique foraging mode and subsequent low amount of time available for nestling defence.

Toepaslike nesplekkeuse en die optrede van ouers en neskuikens teenoor indringers naby die nes is waarskynlik aangepaste gedragseienskappe by 'n spesie waarvan die neskuikens blootgestel is aan predasie. Hierdie studie het gewys dat baie berghaanneskuikens in die Nasionale Krugerwildtuin geroof word en dat berghane blykbaar nesplekke kies waar die neskuikens goed versteek en beskerm is. Die gedrag van ouers en neskuikens veroorsaak blykbaar dat die neskuiken moeilik opspoorbaar is. Daar word voorgestel dat die hoë blootstelling van berghaanneskuikens aan predasie 'n uitvloeisel is van die spesie se unieke jagmetode en die gevolglike klein hoeveelheid tyd beskikbaar om die kuikens te beskerm.

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Nestling predation is the major cause of nesting failure in most birds (Ricklefs 1969) and therefore, any behaviour that reduces nestling predation could increase the individual's lifetime reproductive success and should become prevalent in the population. Birds can reduce nestling predation by making nests less detectable or accessible to potential predators (Skutch 1976), minimize conspicuousness of nestlings or adults at the nest (Knight & Temple 1986), or adults may use distraction behaviours to draw predators away from the nest (Harvey & Greenwood 1978). Thus, it may be predicted that species vulnerable to nestling predation would show some, or all of these behaviours.

Bateleurs (*Terathopius ecaudatus)* lay only one egg and development time of the egg and nestling is unusually long, so breeding is normally attempted only once per season (Newton 1977; Watson 1986) and this rate may be halved because of nestling failure (Watson 1986). Bateleurs now occur only in the larger nature reserves in South Africa (Brooke 1984), where potential nestling predators are abundant, and which closely resemble the environment in which adaptive behaviour may have evolved. In the Kruger National Park for example, terrestrial predators may include any of the larger tree-climbing carnivores or omnivores, such as genet (*Genetta* spp.), African wild cat (*Felis lybica),* chacma baboon (*Papio ursinus)* or tree monitor (*Varanus exanthematicus*). Giant eagle owl (*Bubo lacteus*) and ground hornbiil (*Bucorvus leadbeateri*) are commonly considered to be the larger avian predators of nestlings (Steyn 1982; Kemp & Kemp 1980).

In this paper I show, first, that predation of bateleur nestlings is high, and secondly, that nest site selection and the behavioural responses of adults and nestlings to intruders near the nest conform to the predictions made above. The vulnerabilty of bateleur nestlings to predation is discussed and an inverse relationship between the bateleur's unique foraging mode and time available for nestling defence is proposed.

Study area and Methods

This study was conducted during June 1981 to September 1984 in the Kruger National Park, South Africa. Forty-two bateleur nests were located throughout the Park, and causes of breeding failure at these nests were monitored for the equivalent of 75 pair-years by observing the nest contents at regular intervals throughout the breeding season.

Nest sites were described using variables chosen for their possible influence on nest site selection by bateleurs. The variables measured were of two types. First, those relating to the structure of the nest and nest-tree, which are explained in the results section (Tables 4, 5 and 7, and Figure 1), and second, those variables relating to the vegetation within 100 m radius of the nest-tree which are described below.

The per cent cover of vegetation in five separate height classes around the nest-tree was visually estimated using a seven-point scale similar to the estimates used by Sykes, Horrill & Mountford (1983). The height (measured with a Suunto Instruments clinometer), distance from the nest-tree, and species, of every tree taller than 6 m was recorded for trees within a 100-m radius of the nest tree. The angular dispersion of trees around the nest-tree was estimated by calculating the mean angular deviation, S (Zar 1984). S can vary between 0°, which represents maximum aggregation of trees on one side of the nest-tree, to 81,03° which is maximum dispersion of trees around the nest-tree. The influence of nearest major (tourist) roads, minor (firebreak) roads, permanent water, and water courses (permanent or temporary), was assessed by calculating the mean distance of nest sites to each of them and comparing it statistically with the mean distance from 50 randomly selected points on a map of the area. To avoid bias caused by preferentially locating nests near roads, this comparison was made only in a small, intensively searched study area of 450 km^2 in the central Kruger National Park, in which all adjacent nests were located. Mean distances were compared using the *t* test, with Welch's approximation of *t* with unequal variance where appropriate (Zar 1984).

When possible, nest site variables were compared with their availability in the immediate environment, using a goodness of fit test to detect positive selection versus random use. Otherwise, descriptive statistics were used to simply characterize the variables. Because all variables could not be measured on all trees, the sample size (*n*) is given where necessary.

Behavioural observations of bateleur adults and nestlings at or near the nest were made during visits to the nest to check on breeding status, and from 54 h of observation from a hide at a single nest. Behaviour was described and recorded according to the format proposed by Watson (1986). Breeding status was determined only for pairs known before the start of the breeding season, and productivity measured as the number of successfully fledged young per pair per year (Y/Pr/yr). The cause of failure was deduced from evidence available at the nest site. Failure to lay was assumed for a pair that were seen to be active in the vicinity of the unoccupied previous year's nest, but for which no alternative nest could be located. Failure of eggs to hatch was recorded if the whole egg was known to have been in the nest for more than twice the normal incubation period (de Kock & Watson 1985). A crushed egg was one for which most of the broken shell and contents were found in the nest. Although the act of nestling depredation was never seen, it was inferred from the eaten remains of the nestling in the nest, or signs of predator involvement, such as freshly trampled grass or spoor at the base of the nest-tree. Accidental death was recorded when the undamaged carcass of the nestling was found tangled in the branches immediately below the nest. Death after fledging was recorded when the carcass of the nestling known to have already flown was found below its nest. In some cases the egg or nestling disappeared without sign of cause. Possible causes of mortality in such cases include depredation, or failure to hatch, falling out of the nest, and chilling during bad weather followed by removal by parent or predator.

Results

Causes of breeding failure

Of 75 complete breeding pair-years, 35 pairs successfully reared their young (mean productivity = 0,47 Y/Pr/yr) while the remaining 53% failed. One third of all failures were deduced from evidence at the nest to be caused by depredation of the nestling (Table 1). The cause of egg or nestling loss could not be determined in 22% of the total (Table 1). Failure of the pair to lay was the only other major cause of breeding failure, accounting for 30% of the total (Table 1). Failure to lay may ultimately be caused by low food availability affecting female body condition, although other extrinsic factors may be involved (Newton 1979; Watson 1986). Of the breeding failures that occurred subsequent to egg laying, and for which the cause was known (*n* = 19), 68% were due to depredation.

Behavioural response of adults and nestlings to human and other intruders at the nest

Nests were inspected on 145 occasions during the study period, with nestlings present on 83 occasions, and adults present on 62 and 20 occasions during the incubation and nestling periods respectively (Table 2). On seeing a human approach the nest, nestlings almost always made themselves inconspicuous by crouching below the nest rim (*n* = 78, 94%). Crouching by nestlings also resulted when an adult called and displayed (displays B1 and B2 described by Watson 1986) at another bateleur that intruded into the resident's territory (*n* = 6, from hide observations). On seeing humans approach the nest, incubating adults made themselves inconspicuous by crouching below the nest rim on 30 (48%) occasions, they were seen to leave the nest on 22 (35%) occasions, and were already absent

Table 1 Summary of causes of breeding failure for each year of the study period. *n* = number of failures, % = failures as a percentage of the annual total of failures

	1982		1983		1984		Total	
Cause of failure	*n*	%	*n*	%	*n*	%	*n*	%
Failed to lay	3	43	3	15	6	46	12	30
Egg failed to hatch	1	14	2	10	0	0	3	8
Egg crushed	0	0	1	5	0	0	1	3
Egg or nestling disappeared	0	0	5	25	4	31	9	22
Nestling depredated	3	43	8	40	2	15	13	32
Accidental death of nestling	0	0	0	0	1	8	1	3
Fledged chick died	0	0	1	5	0	0	1	3
Total	7		20		13		48	

Table 2 Frequency matrix of adult and nestling bateleur response to human intruders within 50 m of the nest

Nestling response	Adult response			Adult absent	Sub-total
	Crouch	Leave	Display		
Incubation period					
	30	22	0	10	62
Nestling period					
Crouch	3	14	3	58	78
Aggressive	0	0	0	5	5
Total	33	36	3	73	145

from the nest (possibly detecting my approach and leaving before I saw the nest) on 10 occasions (Table 2).

As both parents forage simultaneously (Watson 1986) adults were rarely seen with a nestling when approached by a human (n = 20, 24% Table 2). On most of these occasions, adults avoided attracting attention to themselves or the nest by leaving the nest area. On only three occasions was an aggressive display (Watson 1986) used against a human intruder. Notably, all three were by the same individual bateleur who repeatedly swooped low over the intruder.

In general, the response of both nestling and adult bateleurs to human intruders near the nest was to make themselves inconspicuous. Intruding conspecifics elicited an aggressive display by adults and crouching by nestlings.

Nest site selection

Eleven of the 21 nest site variables seemed to be important to bateleurs. This was suggested by the variable either occurring more often as a nest site feature than would be expected by random selection of available features, or by occurring frequently within a limited range (i.e. having a low coefficient of variation about the mean value).

Comparison of nest-tree species with tree species available within 100-m radius around the nest-tree (Table 3) showed that overall, bateleurs did not choose tree species randomly, and used *Acacia nigrescens* and *Diospyros mespiliformis* most commonly. The *Acacia* species used (Table 3) are characterized by having many small, hooked thorns which may deter potential predators. *Diospyros mespiliformis* and *Ficus sycomorus* (also used more often than expected, Table 3) are characterized by a well-foliated canopy, which may offer protection by concealment.

Table 3 The use of various tree species for nest sites by bateleurs. Comparison of the frequency of tree species used (F_{used}) for nesting by bateleurs with the frequency of tree species expected to be used (F_{exp}) based on the frequency of tree species available (F_{avail}) within a 100-m radius of the nest-tree (Log-likelihood test). Eight tree species were excluded from the analysis because their F_{avail} was too small for statistical analysis

Tree species	F_{used}	F_{avail}	F_{exp}
Acacia nigrescens	16	147	7,2
Diospyros mespiliformis	8	44	2,2
Acacia welwitschii	3	21	1,0
Ficus sycomorus	2	7	0,3
Combretum imberbe	4	112	5,5
Lonchocarpus capassa	7	132	6,5
Sclerocarya caffra	0	96	4,7
Colophospermum mopane	2	162	7,9
Spirostachys africana	0	26	1,3
Dead tree	0	46	2,3
Total	42	793	

zTree species use was significantly different from expected (G_{adj} = 46,53; *df* = 9; $P < 0{,}01$). Iterative removal from analysis of species with largest difference between F_{used} and F_{exp} showed that *A.nigrescens*, *D.mespiliformis*, *S.caffra* and *C.mopane* were responsible for the significance of the first test, the remaining species used were not significantly different from expected (G_{adj} = 10,9; *df* = 6; $P > 0{,}05$).

Although *S. caffra* was very common in the study area, it was never used as a nest-tree (Table 3). The fruit of *S. caffra* is attractive to a wide variety of animals and is produced at the time when bateleurs are nest building and laying eggs. The subsequent disturbance from foraging animals may cause bateleurs to avoid this tree species. *Colophospermum mopane* was used less often than expected (Table 3) but this was probably an artefact of the small sample size of nests found in *C. mopane* woodland compared with the high tree density in this habitat (Table 3). *Spirostachys africana* trees were also avoided (Table 3). This may be because its profusely branched canopy is impenetrable to any large bird. Dead trees were avoided, possibly because of exposure. *Combretum imberbe* and *Lonchocarpus capassa* were selected randomly. These species do not have thorns, and are not as densely foliated as *D. mespiliformis*. However, they are tall trees and have an open canopy for easy access to bateleurs.

Although there was a large range in tree and nest placement heights used by bateleurs (Table 4a), the coefficient of variation around each feature was low (23% and 27% respectively). Thus, nests were consistently placed at about 73% of tree height (*CV* = 14%, Table 4a), below the tree's canopy.

The height of the nest-tree relative to the height of surrounding trees was of particular importance (Table 4b). All nest-trees were taller than the mean height of surrounding trees, while over 50% of nest-trees were the

Table 4a Characteristics of nest and nest-tree height

	Mean	*SD*	Range	Sample size
Nest-tree height, m	20,1	4,7	12,7 – 36,5	42
Nest height, m	14,7	4,0	9,1 – 26,0	42
Nest height/tree height ratio	0,73	0,10	0,49 – 0,92	42

Table 4b The number of nest-trees taller than, first, the mean height (> mean HST), second, the mean height plus one standard deviation (> mean HST + 1*SD*), and third, the maximum height (> maximum HST) of surrounding trees within a 100-m radius of the nest-tree

	Nest-tree (n = 35)	
	Number	Per cent of total
> mean HST	35	100
> mean HST + 1*SD*	27	77,1
> maximum HST	19	54,3

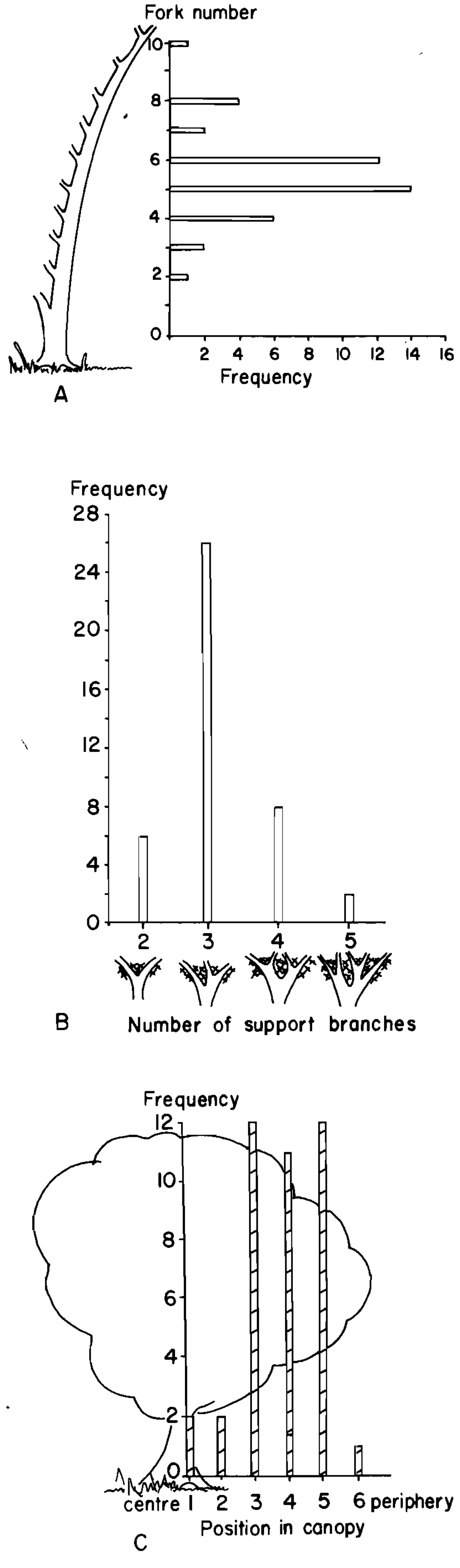

Figure 1 Frequency distribution of nests (n = 42) in relation to the following three nest placement parameters, (A) fork number, (B) number of support branches, and (C) position in the canopy.

tallest tree within the 100-m radius (Table 4b). Thus, bateleurs selected the more prominent trees in the area.

The mean angular deviation, S, of trees about the nest-tree was usually high (mean = 69,8°; SD = 7,1°; n = 35). Thus nest-trees were usually located in an area of fairly evenly distributed trees.

Nest position in the tree was within well-defined limits. All nests were within the canopy. Most nests were in the fifth or sixth fork of the tree (Figure 1A), were supported by three branches (Figure 1B) and were about half way between the tree's centre and its periphery (Figure 1C). These parameters probably covary, so it would be impossible to separate the significance of each. They are probably related to the within-canopy nest placement, and may result from a trade-off between nest stability nearer the centre of the tree versus reduced accessibility to tree climbing predators nearer the periphery of the tree. These aspects of tree morphology may be important to the selection of nest sites, and in turn may influence tree species selected.

Orientation of nests in the tree was significantly different from random (Table 5). Further analysis showed that nests were placed significantly more often in the northern, sun-exposed, side of the tree rather than the east, south or west (Table 5). The majority of nests were shaded within the canopy (69,1%, Table 5), but the rest were exposed for at least ⅓ of the daylight hours. There was no significant effect of exposure on the orientation of nests in the tree (Table 5) so the effect of sunlight on nest placement was small, and the relevance of the northern side placement undetermined.

Within the study area there was no significant difference between the mean distance of nests from major roads and the mean distance of 50 randomly selected points from major roads (Table 6). However, nests were significantly closer to minor roads than the random points (Table 6). A possible explanation of this 'attraction' to nesting near fire-breaks is improved visibility for hunting at a short distance from the nest.

Table 5 Orientation of nest placement, and exposure of nests to the sun

Orientation of nest in tree	Shaded	Exposed
North	11	8
East	5	0
South	10	1
West	3	4
Total	29	13

Nests were unequally placed in the tree with respect to cardinal points (χ^2 = 10,95; df = 3; P < 0,025). Subdivision of the analysis shows that nests were placed in the north quarter of the tree significantly more often (χ^2 = 8,1; df = 1; P < 0,05) than other positions (χ^2 = 2,4; df = 2; P > 0,1). There was no significant orientation of nests in relation to exposure to the sun (G_{adj} = 6,2; df = 3; P > 0,25).

Table 6 Mean distance of bateleur nests ($n = 22$, see text) from major (tourist) and minor (fire-break) roads, permanent water and water courses compared with the mean distances from the same features of 50 randomly located points, in an intensively searched area where all nests were known ($df = 70$ for all tests)

	Distance (km)							
	Nests			Random points				
	Mean	*SD*	Range	Mean	*SD*	Range	*t*	*P*
Tourist road	3,5	2,8	0,10 – 9,0	2,7	1,6	0,01 – 7,7	1,65	> 0,05
Firebreak road	0,8	0,9	0,01 – 3,0	1,9	1,0	0 – 3,5	3,19	< 0,05
Permanent water	1,9	1,3	0,02 – 5,0	2,5	1,2	0 – 5,5	1,48	> 0,05
Nearest water course	0,1	0,2	0,01 – 0,8	0,6	0,6	0 – 2,8	2,18	< 0,05

Main roads are probably too busy to offer this attraction. Although there was no significant difference between mean distance of nest sites and random points to permanent water (Table 6), the mean distance to the nearest water course (either permanent or temporary) was significantly less than that of the 50 random points (Table 6). Water courses may be an attraction because they are preferred hunting habitats (Watson 1984, 1986). It is more likely though, that trees along water courses are preferred because they are generally larger and stay green for longer in the dry season than trees elsewhere.

There was no consistent trend in the use of the remaining variables, which are dealt with briefly below, each having a high coefficient of variation. Nest dimensions (Table 7) varied considerably, suggesting that bateleurs do not have well-defined nest-building parameters. The large standard deviation about the mean branch thickness (Table 7) suggests that, at least above a certain minimum (about 90 mm), branch thickness and therefore nest stability, is not an important parameter.

The amount of cover in the lowest height classes of the surrounding vegetation (< 1 m high) had a bimodal distribution with a wide range of per cent cover, indicating that cover at this level was unimportant. The amount of cover became progressively less as height above ground increased, such that in the 3–10 m and > 10 m height classes the per cent cover was less than 10% and the range small. Thus, nest-trees were generally located in areas with a vegetation profile consistent with open, as opposed to closed, woodland. Similar observations have been made for other large raptors, such as the bald eagle (*Haliaeetus leucogaster*), where open, discontinuous forest stands have been shown to be an important nest site requirement (Andrew & Mosher 1982). The mean density of trees around the nest-tree was 789 trees/km^2 ($SD = 333$ trees/km^2; $n = 35$). The high coefficient of variation (42%) indicates that tree density, within the limits prescribed by open woodland, was not an important factor.

Nests of the redbilled buffalo weaver (*Bubalornis niger*) were found in 28,6% of bateleur nest-trees ($n = 42$). Either an association may exist between the two species, such as mutual protection (physical and cryptic) or they may independently have similar requirements for nesting.

Table 7 Descriptive statistics of nest dimension and support branches, to the nearest 10 mm

	n	Mean, mm	*SD*	Range
Outer diameter	37	880	260	400 – 1500
Inner diameter	25	380	110	300 – 800
Outer depth	37	440	110	250 – 800
Inner depth	25	100	30	30 – 170
Support branches, mean circumference	40	380	110	230 – 750

Discussion

Contrary to raptors in general (Newton 1979), predation of eggs and nestlings was the main cause of breeding failure in bateleurs, suggesting that bateleur nestlings may usually be vulnerable to predation. In general the degree of predation may be affected by the proximity and abundance of particular predators, the amount of time spent away from the nest by parents, or the accessibility and conspicuousness of nests (Newton 1979).

In the Kruger National Park, potential nestling predators are probably abundant, and bateleur parents simultaneously spend a high proportion of the day foraging away from the nest (37% of daylight hours for nestlings less than 42 days old and up to 80% for older nestlings, Watson 1986). The bateleurs mode of foraging is unique among terrestrial birds in that they use low altitude soaring flight, which requires specialized aerodynamics, to search a large area (*ca.* 55 km^2) for carrion (Watson 1986). This method of foraging is time consuming and apparently requires both parents to forage simultaneously in order to provide sufficient food for themselves and their young. I suggest that bateleurs are unable to physically defend their nestling as a consequence of their unique foraging mode which takes them far from the nest for long periods of the day. Thus, the only option for bateleurs to reduce nestling predation is by reducing accessibility and conspicuousness of nests and their contents. This may be achieved by adopting inconspicuous behaviour at the nest, and/or by appropriate nest site selection.

The behavioural response of adults to intruders near the nest was generally to either leave the nest area or crouch below the nest rim, while nestlings generally just crouched. These behaviours may effectively reduce nest detectability to many predators. Other raptors tend to be more aggressive in their nest defence than the bateleur, attacking and sometimes striking intruders (Brown 1976, p. 178), although within a single species the intensity of aggression may vary, and may be modified by past experience (Newton 1979, p.91; Fraser, Frenzel & Mathieson 1985; Knight, Grout & Temple 1987). In other birds the intensity of defence generally covaries with clutch and brood size, and stage of the breeding season (Robertson & Bierman 1979; Greig-Smith 1980). It is tempting therefore, to explain the observed low intensity, or lack of nest defence by the bateleur, as a covariate of its single egg clutch size, by invoking theories of past parental investment and the risk of losing young or future expected benefits (Knight & Temple 1986). However, the idea that bateleurs are unable to defend the nestling because they are absent from the nest for long periods is a more simple and very plausible explanation for behaviours that reduce nest detectability. In addition, contrary to the prediction from nest defence theory (e.g. Knight & Temple 1986) that bateleurs would be less assertive further from their nest than nearby, breeding bateleurs can be very aggressive toward conspecifics as well as other raptors, when at a distance from the nest (usually more than 1 km, Watson, in press a & b).

Bateleurs occupy nest sites that are distinctive to the species (Moreau 1945; Brown 1955; Steyn 1965, 1980; Tarboton & Allan 1984), indicating that certain features of the site are repeatedly selected. This study has shown that the thorny acacias, or the well-foliated tree species were used for nest sites more often than expected. Other variables which showed low variance were related to the common phenomenon of the nest being placed below the canopy. Sites were also selected to be near water courses where trees were taller and remained green for longer than elsewhere. This frequent selection of nest site features that conceal and protect the nest and its contents from predators, combined with the consistently unassertive response of adults and nestlings to intruders near the nest, supports the notion that appropriate selection of nest sites and behaviour at the nest might increase the individual's lifetime reproductive success and has therefore become prevalent in the population.

Further evidence is provided by contrasting the use of concealed nest sites by bateleurs against those of other large African raptors with different foraging modes and prey type, such as the martial eagle (*Polemaetus bellicosus*), tawny eagle (*Aquila rapax*), African hawk eagle (*Hieraaetus spilogaster*), crowned eagle (*Stephanoaetus coronatus*), African fish eagle (*Haliaaetus vocifer*), snake eagles (*Circaetus cinereus, C. pectoralis*) and vultures. These species generally build large and/or conspicuous nests (Steyn 1982). The difference in nest site selection between these species and the bateleur may be related to the degree of nestling vigilance and defence provided by parents, which in turn is inversely proportional to the total time required and area covered by the parents for foraging and other maintenance activities, such as territorial defence (Watson 1986). For example, raptors that kill their prey may have a relatively smaller home range, and can more readily observe and defend their nest, than carrion feeders that predominantly search over a large range. Sit and wait foraging within a relatively small range by the African fish eagle may allow the parents to constantly observe and protect their nestling, without necessarily sitting at the nest itself (nest attendance is low, Steyn 1982). Whereas killing prey may be less time consuming than searching for carrion, the facultatively co-operative foraging by griffon vultures (Houston 1974) may allow parents of these species the time to alternately attend the nestling. In contrast, the bateleur's foraging mode of individually searching for small carrion items over a large home range (Watson 1986) is time consuming and limits the time available for nestling vigilance and defence. However, testing the theory of an inverse relation between foraging-mode/prey-type and time available for nestling defence requires directly comparative information on a wider variety of raptors than is currently available.

A test of the adaptiveness of nest site selection may be possible if the variables on which selection is based lie on a continuous scale from preferred to avoided. If so, then one may expect some sites to be more productive than others, resulting in a dichotomous or continuous scale of breeding success, as found in ospreys (*Pandion haliaaetus*; Ames & Mesereau 1964), merlins (*Falco columbarias*; Newton, Meek & Little 1978) and northern harriers (*Circus cyaneus*; Simmons & Smith 1985). Thus, testing the prediction that nest site selection is adaptive in bateleurs would require location of nests in areas where suitable sites are limited, such as may occur in landscapes within the Kruger National Park (e.g. mopane shrubveld, Gertenbach 1983) where tall trees are limited to water courses and the latter are sparsely distributed. Productivity and the causes of breeding failure could then be compared between nests of differing suitability. However, elsewhere in southern Africa, bateleurs have been extirpated from suitable habitats through human activities (Tarboton & Allan 1984; Watson 1986, 1987) so suitable nest sites are unlikely to be limited.

Nest site selection is important to the species population ecology because it will have a limiting effect on the species distribution and abundance where suitable nest sites are limiting (Newton 1979). In addition, the quality and number of sites within a territory may affect the species productivity (e.g. Simmons & Smith 1985). Further research in which the number and quality of suitable nest sites are compared with breeding density and population productivity would yield information relevant to understanding the species' population ecology and therefore relevant to their conservation management in southern Africa.

Acknowledgements

This research was funded by the FRD section of the CSIR, the South African Ornithological Society, South African Nature Foundation, and the University of the Witwatersrand. The National Parks Board of Trustees is thanked for allowing me to work in the Kruger National Park. I am especially grateful to Chris Watson for field and technical assistance as well as comments on earlier drafts of this manuscript. I am grateful to Joe Henschel for his translation of the abstract.

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