

Flight, foraging and food of the Bateleur *Terathopius ecaudatus*: an aerodynamically specialized, opportunistic forager

R. T. Watson

ABSTRACT

The low altitude, soaring flight of the Bateleur *Terathopius ecaudatus* is unusual and characteristic of the species. Wing and tail measurements showed that their aspect ratio (8:1) is only slightly higher than other soaring raptors (7:1), but their relative tail length is considerably less (Bateleur tail:wing-length = 0.2, other eagles >0.4). Observations of Bateleur behaviour showed that foraging was performed from low altitude soaring, in which a limited range (45-55 km²) was repeatedly searched for up to 70% of daylight hours. Strikes at prey (n = 229) were conspicuous and at slow speed. Analysis of prey remains showed that prey was either carrion or, possibly captured live, was nocturnal mammals, reptiles, or insectivorous birds. Feeding trials (n = 40) showed that Bateleurs were adept at locating small-sized carrion (67% of 131 baits) and were first on 94% of occasions. I hypothesize that the specialized aerodynamics of Bateleurs allows them to soar and forage at low altitude, to opportunistically take carrion and live prey, and thus to occupy a food niche that apparently is used rarely by other diurnal avian scavengers.

INTRODUCTION

The flight of the Bateleur *Terathopius ecaudatus* is often mentioned as an extraordinary and identifying characteristic of the species (Watson 1987, Brown & Amadon 1989, Tarboton 1990). Their low altitude, canting flight (Pennycuick 1972) is shared with few other raptors and their relatively long, narrow wings and short tail are unique among terrestrial birds (Watson 1986). The relationship between these characteristics and their natural history has not been thoroughly explored. In this paper I describe and quantify pertinent aspects of the Bateleurs' flight, foraging and food, and propose a relation between their morphology, aerodynamics, foraging behaviour and diet.

METHODS

This study was conducted between 1981 and 1984 in the Kruger National Park (KNP, 22°32'-25°32'S; 30°50'-32°02' E), South Africa. The KNP is just over 350 km long, 90 km wide at its widest, and covers an area of about 20,000 km². Habitat within the KNP is generally described as eastern lowveld and can be divided into several landscape types (Gertenbach 1983). Most behavioural

observations occurred in the central part of the KNP, within a 15-km radius of Satara rest camp, and in two landscapes known respectively as *Acacia welwitschii* Thicket and *Sclerocarya caffra*/*Acacia nigrescens* Savanna.

Flight

Bateleur flight behaviour was studied by 'focal bird observations' of known individuals from two high vantage points (a rock outcrop called Matikiti Kopje and an unnamed rock outcrop on the Sweni River) that allowed up to 3 h of uninterrupted observation per individual. Two adjacent territorial pairs were observed from each point for 192 h between 1982 and 1983. Individuals were readily identified by their sexually dimorphic plumage and their visits to known nests.

Birds were observed through a 25-50x zoom spotting scope. At 1-minute intervals the focal bird's horizontal distance from the observer was visually estimated to the nearest 0.5 km using landmarks of known distance, its magnetic compass bearing measured from a sighting compass mounted on the telescope, and its behaviour described. Data were recorded on a tape recorder for later transcription so that the observer never lost sight of the focal bird.

Focal bird flight direction was calculated from successive locations, assuming that travel was in a straight line between locations at one-minute intervals. Home ranges were measured by plotting successive, sub-sampled, statistically independent (Schoener 1981) locations of observed birds. Convex polygons were drawn around outermost locations and the map-maker's formula used to calculate the polygon area.

Foraging

Foraging behaviour was recorded during the same focal bird observations described above. In addition, observations of every Bateleur seen and recorded during the study period ('ad-libitum' observations, $n = 4255$ from 1981 to 1984) were used to increase sample sizes of rarely seen behaviours, such as attempted and successful strikes at prey.

Food

Diet was determined by identification of prey remains collected at nests and from birds observed feeding during focal bird and ad-libitum observations. Prey remains were either 'bulk' items such as skin, bones, scales and feathers, or they were pellets. Feathers were only considered to have come from prey if more than one was found below the nest, otherwise they were disregarded as being moulted. The numbers of each prey type were conservative minima because as many pieces as possible from each sample were combined to represent one prey item and only parts clearly belonging to different individuals were counted separately.

Mammal remains were identified to species, if possible, otherwise they were placed into an ungulate size class suggested as appropriate for the classification of antelope bone remains (Brain 1974). Bird remains, feathers, bones, mandibles and claws were identified to family, as were reptile and fish parts (mainly skulls, skin and scales).

Pellets were dissected dry and separated into component parts for identification. Mammal hair was identified to species, using gelatin impressions of scale patterns that were compared with reference collections (Keogh 1974, 1979, 1983). Feathers and other bird parts were identified macroscopically from reference collections. Reptile scales were identified based on shape, colour, presence of apical pits, ridges or spines and calcification using museum reference collections. Fish scales were classed simply as unidentified fish. Insect parts were identified to order where possible from reference collections.

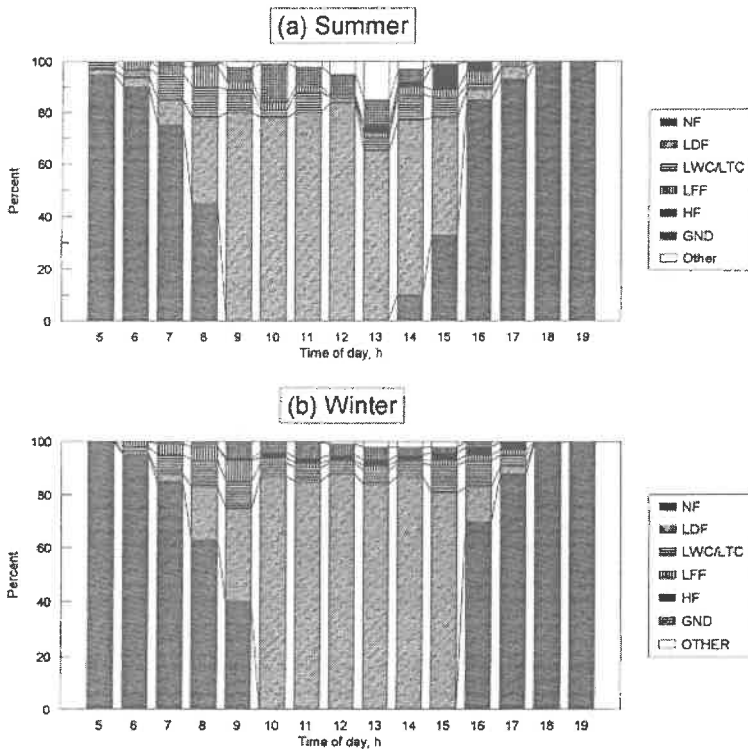
The importance to diurnal scavengers of small items of carrion (fist-sized lumps of meat or other carrion of similar size) was measured experimentally by setting meat baits in plain view, then watching them from a concealed vantage point until the first animal arrived and ate the bait. Two or three baits, each >150 m apart, were usually put out around 08:00 hrs, after Bateleurs began flying, and observed simultaneously until discovered by scavengers or until dusk.

RESULTS

Flight

Bateleur flight was distinguished by continuous low-altitude soaring flight (low directional flight, LDF, Fig. 1, Watson 1986), at elevations of roughly 2-3x tree-top level (about 40-80 m above ground level, a.g.l.). Flight from the ground or elevated perch usually began with a brief period (e.g. 10 - 30 seconds) of flapping flight (FF, Fig. 1), but proceeded thereafter for long periods (e.g. 10 - >360 minutes) without flapping. Soaring Bateleurs exhibited a characteristic irregular canting motion of the wings, that resembled movements expected of an unstable aircraft or bird which must frequently correct its flight attitude (roll) as it flies through turbulent air. Low wide- or low tight-circling (LWC, LTC, Fig. 1) occurred occasionally during flight, often associated with loss of height as the bird appeared to inspect potential prey on the ground. Circling in thermals (thermallings) to gain height was most often seen in the afternoon, associated with high flying (HF, Fig. 1) at much higher elevations than low flight and often exceeding 300 m a.g.l..

Figure 1. Bateleurs' diurnal activity pattern in (a) summer and (b) winter from focal bird and ad-libitum observations combined. NF = non-flying. All other abbreviations described in the text.



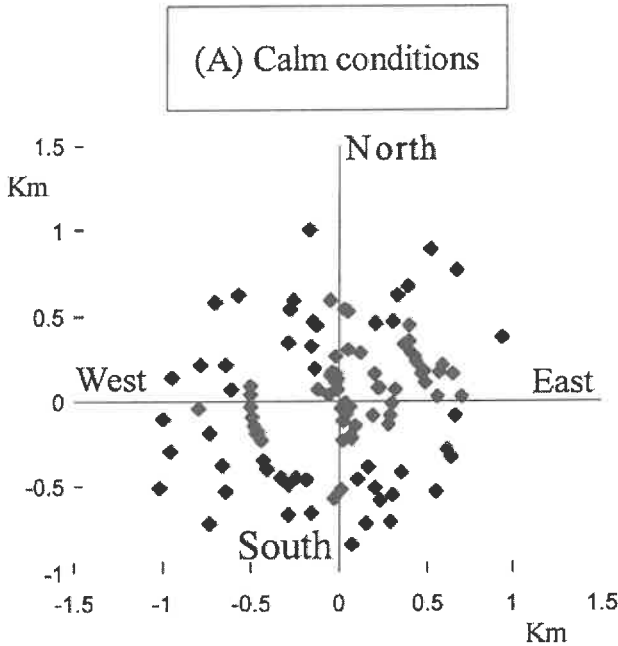
Diurnal activity patterns for summer and winter (Figs. 1a & 1b respectively), derived from focal bird and ad-libitum sampling, revealed that the majority of Bateleurs began flying about 2-3 h after sunrise, and continued for 6-8 h until 2-3 h before sunset. During this active period of 50-70% of daylight hours, most time (40% of daylight hours in summer and 57% in winter) was spent in low directional soaring flight (LDF, Fig. 1). Much smaller proportions of time were spent in low wide

circling (LWC), low flapping flight (LFF), high flight (HF), on the ground (GND) or other activities (Other, Fig. 1). Activities on the ground (GND, Fig. 1) included feeding and bathing. Flight began and peaked earlier in the day in summer than in winter, suggesting a dependence on heating by the sun to generate thermal energy for soaring flight. Flight terminated earlier in the day in summer than winter, suggesting that termination of flight was not solely determined by thermal factors, but also possibly social behaviour or satiation.

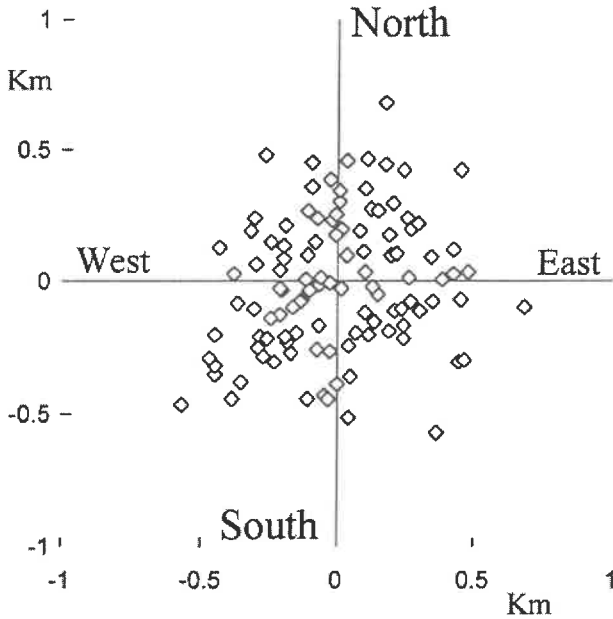
Low directional flight speed was crudely measured by driving a vehicle at the same speed as a Bateleur as it flew over or parallel to a road. Opportunities to do this occurred fortuitously 3 times during the study period and all measured a ground speed of 50-60 km/h. By inference, Bateleurs could travel 250-480 km in low directional flight in a normal activity period of 6-8 h.

Focal bird observation revealed that Bateleur pairs used low directional flight to repeatedly traverse a limited home range of 45-55 km² ($n = 4$, mean = 51.6 km², SD = 4.8) measured by the convex polygon method. Flight direction was measured from successive 1-minute interval locations during focal bird observations of the same individual under strong wind (>25 knots) and calm conditions (Fig. 2). Flight direction was not significantly different from random or uniform under either strong wind (Rayleigh's $z = 1.57$, $n = 110$, $P = <0.05$) or calm conditions (Rayleigh's $z = 0.10$, $n = 109$, $P = <0.05$, Zar 1984).

Figure 2. Flight directions and distances of one individual Bateleur in (A) calm and (B) windy conditions.



(B) Wind conditions



Foraging

Strikes at prey and descents to carrion by Bateleurs were observed 229 times during focal bird and ad-libitum observations combined. Three types of prey strikes and one type of descent to carrion were readily distinguished. 'Kill Strike-A' began with low tight circling followed by a wings up, slow descent onto prey on the ground. 'Kill Strike-B' was a slow descent, with wings held out to break the descent, to land in a tree, apparently capturing arboreal prey. 'Kill Strike-C' began with a fast, shallow dive below tree-top level, followed by recovery in flight with prey in the talons. This was seen once, and was the only attempt at prey capture in flight. 'Approach to carrion' began with low tight, or low wide circling, followed by landing on the ground or on an elevated perch at a distance from the carrion, followed by landing on or walking up to the carrion. Apart from Kill Strike-C, all strikes and approaches to carrion were slow and conspicuous, requiring a wings-up ('parachute-like') descent and wing flapping to break the descent just before touch down. Kill strikes or descents to carrion were always associated with low flying. The temporal pattern of foraging was illustrated in the daily activity pattern (Fig. 1) by all low flying and ground activity combined. Change in foraging success and foraging effort through the day was illustrated by indices derived from observations at feeding trials. A foraging success index was calculated as the difference between the number of baits found and the number expected to be found based on the proportion of bait-hours available (Table 1). An index of foraging effort was calculated from the number of baits located by Bateleurs per bait-hour (Table 1). Indices of foraging success and foraging effort before 08:00 hrs and after 16:00 hrs were too influenced by small sample size to be meaningful. Otherwise, foraging success was positive during 10:00-13:00 hrs and greatest from 10h00 to 11h00, while foraging effort was greatest during 10:00-12:00 hrs but remained high and fairly constant until 16:00 hrs (Table 1).

Table 1. Temporal distribution of foraging success and effort by Bateleurs determined from feeding trials with baits.

<i>Time of day</i>	<i>No. of bait hours, h</i>	<i>No. of baits found (bf)</i>	<i>No. of baits expected to be found (bef)</i>	<i>Foraging success index, (bf-bef)</i>	<i>Foraging effort index, (bf/h x 100)</i>
07h01-08h00	7	1	0.9	0.1	15.4
08h01-09h00	75	6	10.4	-4.4	8.0
09h01-10h00	182	12	25.2	-13.2	6.6
10h01-11h00	203	40	28.1	11.9	19.7
11h01-12h00	187	33	25.9	7.1	17.7
12h01-13h00	154	24	21.4	2.6	15.6
13h01-14h00	129	16	17.9	-1.9	12.4
14h01-15h00	83	10	11.5	-1.5	12.1
15h01-16h00	33	4	4.6	-0.6	12.1
16h01-17h00	3	1	0.4	0.6	33.0
Total	1046	145	145		

Food

Analysis of Bateleur prey remains revealed 1,879 individual items, including 49 mammal species, 37 bird species, 20 reptile species, 5 fish genera, one unidentified frog, and two arthropod genera (Table 2). Any identified mammal normally weighing over 5 kg was assumed to have been picked up as carrion (Table 2). Mammals weighing less than 5kg were assumed possibly to have been captured, as were all birds, reptiles and fish, although the latter probably only became available with the seasonal drying up of dams and rivers.

Table 2. Summary of prey identified in prey remains from all known Bateleur nests in the KNP in 1982 and 1983. Identifications to species were given by Watson (1986).

	<i>Frequency</i>	<i>Percentage</i>
Mammal		
Carrion	681	36.2
Captured	346	18.4
Sub-total	1027	54.6
Bird	446	23.7
Reptile	334	17.8
Fish	37	2.0
Unidentified & other	35	1.9
Total	1879	100%

Mammalian carrion comprised the single most frequent food source (Table 2). The most frequent (>10 individuals) species included Blackbacked Jackal *Canis mesomelas*, Porcupine *Hystrix africaeaustralis*, Greater Canerat *Thryonomys swinderianus*, Cape Buffalo *Syncerus caffer*, Bushbuck *Tragelaphus scriptus*, Impala *Aepyceros melampus*, Common Duiker *Sylvicapra grimmia*, and Steenbok *Raphicerus campestris*.

Of the animals small enough to have been killed, birds were the most frequent prey item, most often (>10 individuals) including Cape Turtle Dove *Streptopelia capicola*, other dove species, Green Pigeon *Treron calva*, Lilacbreasted Roller *Coracias caudata*, Redbilled Woodhoopoe *Phoeniculus purpureus*, Yellowbilled Hornbill *Tockus flavirostris*, Burchell's Starling *Lamprolornis australis* and other glossy starlings.

Small mammals were the next most frequent prey item (Table 2), often (>10 individuals) including Cape Hare *Lepus capensis*, Scrub Hare *L. saxatilis*, Multimammate and Coucha Mouse *Praomys* spp., Veld and Rock Mice *Aethomys* spp., Bushveld Gerbil *Tatera leucogaster*, Pouched Mouse *Saccostomus campestris*, Small- and Large-spotted Genet *Genetta* spp., Slender Mongoose *Herpestes sanguineus*, and Dwarf Mongoose *Helogale parvula*.

Reptiles were almost as frequent in the diet as small mammals (Table 2), and often (>10 individuals) included various skink species, lacertid species, Plated Lizard species *Gerrhosaurus* spp., Cordylidae species, Nile Monitor *Varanus niloticus*, Olive Grass Snake *Psammophis phillipsii*, Puff Adder *Bitis arietans*, Black Mamba *Dendroaspis polylepis*, and other unidentified snake species. Amphibians and invertebrates were identified but represented <0.1% of the total. The extremely high diversity of small and possibly killed prey items in the Bateleurs' diet, plus the abundance of obviously carrion items, suggests that Bateleurs are primarily scavengers and that some or many of the small prey items may not have been killed but were scavenged as carrion.

Of 131 baits put out during 40 separate feeding trials, 94 (72%) baits were found by scavengers (Table 3). Bateleurs found 67% of all baits put out (40% adults, 60% non-adults included in four age-classes recognizable before adult, Watson 1987), and they were the first diurnal scavenger to find the bait on 94% of occasions (Table 3). Bateleurs were relatively more efficient at finding these small baits than they were at finding large carcasses, as observed by Mundy (1982) at which Bateleurs were first to arrive at only 47% of 91 carcasses.

Table 3. Species and numbers of scavengers that were first to arrive at baits that were located (n = 94) compared with all the baits observed (n = 131).

<i>Species</i>	<i>Number of baits located by scavengers</i>	<i>Percent of baits located by scavengers</i>	<i>Percent of all baits observed</i>
Bateleur	88	94	67
Whiteheaded vulture	2	2	2
Blackbacked jackal	2	2	2
Slender mongoose	2	2	2
Total	94	100%	73%

Bateleurs were seen eating, catching or carrying prey on 71 occasions during focal bird and ad-libitum observations. Of these, 70% and 85% of all items taken by adult and non-adult Bateleurs respectively were deduced to be carrion (Table 4). About 20% of the diet was large carrion items (>5 kg live weight), and 54% small carrion, such as dead birds, reptiles, and other small animals killed on the roads or in the grass fires that annually burn in savanna landscapes (Table 4). The remainder were live prey.

Table 4. Diets of adult and non-adult Bateleurs determined from focal bird and ad-libitum observations. Live-captured vs. carrion prey were deduced from the Bateleur's behaviour (Watson 1986) or direct observation.

<i>Prey type</i>	<i>Adult frequency</i>	<i>Non-adult, frequency percentage of total</i>	<i>All age classes</i>
Carrion			
Large carrion	10	4	20
Small carrion			
Bird	1	1	3
Reptile	2	0	3
Unidentified	20	10	42
Road kill	2	2	5
Burn kill	0	1	1
Sub-total	25	14	54
Total carrion	35	18	74
Live prey			
Small mammal	5	1	9
Bird	1	1	3
Reptile	8	0	11
Termites	1	1	3
Total live prey	15	3	26
Grand total	50	21	100

DISCUSSION

Soaring is a low energy method of flight (Pennycuick 1980) that is used widely among terrestrial and marine birds. Most terrestrial soaring birds use thermals as the source of lift for directional soaring flight. They circle to gain altitude in a thermal then glide, losing height between thermals (Pennycuick 1972). Alternatively, they can fly continuously in one direction by slowing their forward speed in a thermal while rising, and speeding-up in areas of sinking air to minimize altitude loss (Pennycuick 1972). In this way they maintain or even gain altitude while moving forward. Slope and undulating air currents are also used for lift when a strong and constant breeze is available (Rüppell 1977). The low altitude soaring flight of the Bateleur, without circling in thermals and under conditions of calm to light breeze, is therefore unusual among soaring birds.

Pennycuick (1972) explained the characteristic flight of Bateleurs as a form of dynamic soaring, in which they extract energy from horizontal gusts of air in the manner of sea birds, such as albatrosses (Rüppell 1977). One way this could be done is to bank alternately right and left, showing the raised wing to the swell (Pennycuick 1972). This explanation implies that wing canting by the Bateleur should be a fairly regular rocking motion and it is probable that this form of dynamic soaring alone would impose restrictions on the Bateleurs' direction of flight relative to the prevailing wind direction. To fly in another direction, they would be forced to use thermals in a manner similar to vultures (Pennycuick 1972). Careful observation of Bateleurs in flight revealed an erratic canting motion, resembling a bird's reaction to instability. Focal bird observations showed that Bateleurs' direction of flight was random or uniform and independent of wind direction (Fig. 2). It also showed that thermal soaring occurred most often only in the late afternoon, after hunting and other maintenance activities were accomplished for the day (Fig. 1). Therefore, Pennycuick's (1972) explanation of Bateleur flight would seem to be only a partial explanation.

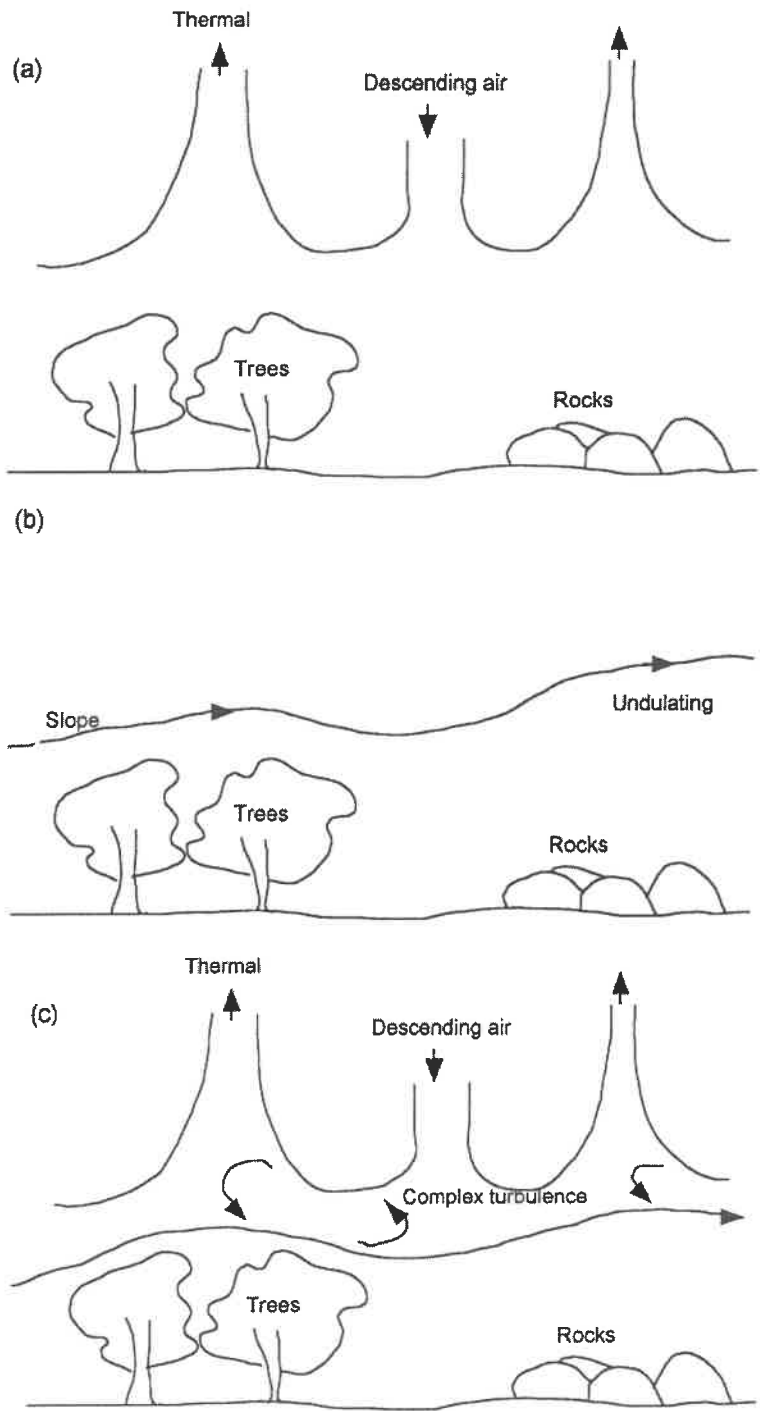
I propose the following hypothesis as a possible explanation for Bateleur flight. At low altitude, under normal conditions of calm air to light breezes, sources of lift are probably not well defined. Air moves horizontally between areas of rising thermals and sinking air (Fig. 3a), and weak slope updrafts and undulating air (Fig. 3b), superimposed on thermals, add complexity, unpredictability and turbulence to conventional sources of lift (Fig. 3c). Irregular wing canting by Bateleurs in soaring flight resembles the motions expected of a bird in turbulent air.

For a bird to soar in any direction at this altitude, it must detect and use the slightest sources of lift and speed up through areas of sinking air. If this were so, Bateleurs would gain and lose altitude repeatedly as they flew, perhaps shifting from one state to the other so rapidly as to be unnoticeable. I suggest that the Bateleur is capable of using weak sources of lift found at low altitude that, because of its uniquely specialized aerodynamics, described below, are useless to other terrestrial soaring birds.

Efficient gliding aircraft are designed to fly in such a way as to maximize their glide ratio (forward distance to sinking distance), by obtaining maximum lift with least drag. Drag is most readily reduced by increasing the aspect ratio (wing-length:wing-width) because more elongated and pointed wings generate less induced drag (Rüppell 1977). Such a design would also be efficient for soaring birds, but it is severely limiting for other aspects of their survival. Long thin wings would be difficult to manoeuvre in confined spaces, such as negotiated by most terrestrial birds, and takeoff and landing would be increasingly difficult. Wing design of soaring birds represents a compromise between efficient gliding and other essential capabilities.

Albatrosses inhabit the marine environment, where wing length is less limited by confined space, and so come closest to the long thin wing design of efficient gliding aircraft. The aspect ratio of the Wandering Albatross *Diomedea exulans* is 20:1 (Brown 1976, Rüppell 1977), and is much greater than the aspect ratio of the Bateleur (8:1) or White Backed Vulture *Gyps africanus* 7:1 which has a glide ratio of 15:1 (Pennycuick 1972). Being limited by terrestrial confinement, the Bateleur's wing dimensions are only slightly modified to increase aspect ratio for efficient soaring.

Figure 3. Diagrams of (a) thermals that may be used by Bateleurs to gain lift at low altitude in the absence of a breeze, (b) other sources of lift at low altitude, that may be created by a light breeze, and (c) complex sources of lift at low altitude.



I suggest, therefore, that the Bateleur's unique ability to soar at low altitude, without using thermals, may also be attributed to its unusually short tail, an aerodynamic modification not found in other raptors. The Bateleur's tail-length:wing-length ratio is 0.2, whereas that of all other raptors are greater than 0.4 (Brown 1976).

The aerodynamic effects of tail length and shape have not been accurately measured for any bird, but it seems to be generally assumed that the tail mainly serves a stabilizing and directional function. The tail also provides lift and is a source of drag (Tucker 1992). The Bateleur's tail has a small surface area and presumably generates relatively little drag. Low drag would improve the glide ratio and, thus, may allow Bateleurs to use weak sources of lift. However, the tail also produces lift, so the short tail of the Bateleur must represent a trade off between better lift and loss of drag. For the Bateleur less drag seems to be the more important factor.

Compared with other raptors, the Bateleur's very reduced tail length and area has an obvious impact on its method of foraging. For example, a Black Kite *Milvus migrans*, which is readily seen manoeuvring in close proximity to humans, can be seen to twist, fan or angle the tail, to turn in confined spaces without rapid forward flight, and to land precisely on small targets. The tail is also used as an air-brake; when fanned and angled forward it rapidly halts a bird after a stoop at prey. If spread while hovering, the tail provides an extra lift-producing surface, like the wing-flaps on an airplane.

The Bateleur's reduced tail length must affect essential hunting abilities by reducing its ability to manoeuvre in close quarters and at slow airspeed, to brake after a stoop or to hover. It may also reduce stability in normal gliding flight (Rüppell 1977) and this may contribute to the Bateleur's irregular canting motion while flying. Presumably these abilities are important to most other raptors' survival and propagation, as no other raptors have a tail as short as the Bateleur.

The effect of a short tail can be readily seen in the Bateleur's typical approach to prey (Kill-Strikes A and B, and Descent to Carrion). The effect of a short tail was most obvious in the birds' dependence on wing-flapping to stop, but it also necessitated a slower approach with wings held up rather than tucked in for a fast stoop. This, combined with the circling before the stoop, must eliminate for Bateleurs any element of surprise that is used by other avian hunters to their advantage.

Low altitude soaring was used principally for foraging by the Bateleur and must compensate for its apparently clumsy hunting and killing method. I suggest that flying for long periods of time, repeatedly searching a limited home range of 45-55 km² at low altitude, brings Bateleurs into contact with an unusual food supply, namely small-sized carrion. The detailed searching allowed by low altitude soaring probably means that Bateleurs can see small dead animals that other avian scavengers, flying at higher altitude, cannot detect. Because Bateleurs are smaller than and subordinate to most other avian scavengers, preferring to leave a large carcass when they arrive (Houston 1980, Mundy 1982, Watson & Watson 1987), small carrion that can be consumed quickly by the Bateleur may be an important food source.

Feeding trials demonstrated that Bateleurs are very efficient at finding small items of carrion. Prey remains showed that at least 36% of the diet was large carrion, and ad-libitum and focal bird observations indicated that this proportion may be as high as 74%, including at least 54% small carrion.

However, Bateleurs also killed live prey (Steyn 1980, Watson 1986) and their low altitude searching can bring them into contact with many small animals. The most frequent small prey species could be described collectively as nocturnal mammals, insectivorous birds and various reptiles. I propose that the common denominator among these prey groups is that they may have to be temporarily occupied or distracted, such as insectivorous birds killing their own prey, nocturnal mammals disturbed from their diurnal lairs, or sun-basking reptiles, for the Bateleurs' approach to be effective.

In conclusion, I propose that the unique flight of the Bateleur, its foraging method and food source are linked. Bateleurs appear to be opportunistic foragers that are aerodynamically specialized, by virtue of their short tail and slightly higher aspect ratio, for low altitude soaring for long periods of time. This flight mode brings Bateleurs into contact with small carrion and temporarily distracted mammals, birds and reptiles, often enough to be an important and consistent source of food that is little exploited by other diurnal scavengers.

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Richard T. Watson
The Peregrine Fund
World Center for Birds of Prey
566 West Flying Hawk Lane
Boise, Idaho 83709
U.S.A.

