# Aggressive display and territoriality of the bateleur *Terathopius ecaudatus*

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Bateleurs exhibit an aggressive display to conspecifies that incorporates an 'attack' pattern; the display has a territorial function because it drives intruders away from the nest, usually by a gain in altitude by the intruder. Resident breeding adults typically displayed at adults of the same sex or any of the non-adult age-classes, and each sex displayed equally often. The intensity of adult aggression was highest during the incubation period and decreased thereafter. Territories were maintained throughout the year, even after breeding failure and in non-breeding years. Bateleurs seem to maintain territories mainly for feeding, but other causes of territory formation, such as mate, progeny or nest-site protection, are not discounted. The intensity of adult aggression towards non-adults may influence non-adult movements, local distribution, and abundance. Aggression by non-adults was infrequent and was considered to be 'play' behaviour.

Berghane vertoon 'n aggressiewe houding teenoor gelyksoortiges, wat 'n aanvalspatroon insluit. Die houding het 'n territoriale funksie aangesien dit indringers van die nes verdryf, gewoonlik deur 'n vermeerdering·in hoogte. Lokale broeiende volwassenes vertoon die houding normaalweg teenoor volwassenes van dieselfde geslag of enige van die nie-volwasse ouderdomsgroepe, en albei geslagte vertoon ewe dikwels. Die intensiteit van volwasse aggressie was die hoogste gedurende die broeiperiode, en het daarna verminder. Territoriale gebiede is deur die jaar gehandhaaf, selfs na mislukte broeipogings en ook in jare wat hulle nie gebroei het nie. Dit skyn of berghane territoriale gebiede handhaaf hoofsaaklik vir voeding, maar ander redes, byvoorbeeld paring, of die beskerming van kleintjies of die nesgebied, word nie buite rekening gelaat nie. Die intensiteit van volwasse aggressie teenoor nie-volwassenes mag die bewegings, plaaslike verspreiding, en hoeveelheid van nie-volwassenes beïnvloed. Aggressie deur nie-volwassenes was seldsaam en word as 'speelgedrag' beskou.

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The territorial function of displays by raptors has often been subjectively interpreted without knowing the context of the display, and this has lead to the possible misinterpretation of displays, such as undulating flight in golden eagles *Aquila chrysaetos,* and aerial cartwheeling in bald eagles *Haliaeetus leucocephalus* (Harmata 1982). In studies of territoriality it is important to distinguish territorial aggression from other displays because similar displays may have different functions (e.g. territorial aggression vs. courtship) that depend on the context of the display (Hinde 1970; Wallace 1979).

Aggressive displays by the bateleur *Terathopius ecaudatus* are most often directed at conspecifies and incorporate an 'attack' behaviour pattern (dive to within contact distance of a second bird and present talons) and other patterns used in association with 'attack' (Watson 1986). The aim of this paper is to deduce the function of the aggressive display of the bateleur with reference to the context in which it occurred. The context was determined from which individuals (sex and age class) were either aggressors or defenders, when the aggression occurred, and the outcome of the behaviour. Bateleurs are particularly good subjects for this kind of study because, unlike many raptors, their sex and age class ('non-adults' in this paper refers collectively to juvenile, immature, sub-adult, and pre-adult age classes; Brown & Cade 1972) are easily determined from field observations.

## Methods

Two methods of behavioural observation were used in this study, which was conducted in the Kruger National Park, South Africa. I recorded the behaviour of every bateleur I saw in the field, also noting the bird's age and sex, the time of day and the time spent sampling. This method approximates instantaneous sampling (Altmann 1974; Tarboton 1978). Between 1981 and 1984 I made 4 015 sightings.

During 1983 I also used focal animal sampling (Altmann 1974), in which individual bateleurs were observed continuously over a period of time to determine the context in which a behaviour occurred. Eight resident bateleurs were observed from two elevated points, located in the central Kruger National Park (24°40'S / 31°50'E). From both points the nest sites of two adjacent pairs could be seen, and the birds' activities over their entire home range observed. Observations were made for three consecutive days at each observation point every month. Focal birds were observed for a total of 172 h: 16 h between 08h00–10h00, 54 h between 10h00–12h00, 59 h between 12h00–14h00, 38 h between 14h00–16h00, and 5 h between 16h00–18h00.

The focal bird was observed from distances up to 8 km through a 25-50 × zoom telescope mounted on a tripod, and observations were recorded on a tape recorder. An audible time signal was used to time behavioural events to the second and a compass mounted above the eyepiece allowed bearings to be taken with minimal break of visual contact with the subject. Visual contact was readily restored after such readings because focal birds were usually silhouetted against the sky. On first sighting an adult bird, I noted its sex (distinguished by sexually dichromatic plumage pattern), activity at that moment, compass bearing, range (visually estimated relative to ground features at known distances), and the time of day. Thereafter, at 1-min intervals, I recorded the bird's compass bearing, range and activity at that moment, and the sequence and duration of activities during the previous minute. The bird's activity was categorized from a catalogue of behavioural acts and patterns I had previously observed (Watson 1986). The focal bird was observed for as long as it remained in sight or until observer fatigue became significant (0,5–3,0 h).

Two of the eight birds were individually recognizable from unique plumage irregularities. The other six birds could not be recognized immediately. However, during preliminary observations made in 1982, I established that bateleurs could be identified as resident individuals if they flew directly over or visited a nest (Watson 1984). Furthermore, a resident pair's home range overlaps only slightly with the adjacent pairs' home ranges (Watson 1984, 1986). Therefore, if a bird was watched for 30 min or more, it usually flew over enough of its home range to allow determination of the pair to which it belonged. The identity of the bird was not established on only 12 out of 223 focal-bird observation periods and these were excluded from data analysis.

## Results

The majority (87%) of 185 aggressive displays observed by instantaneous sampling were initiated by adult birds (Table 1) which represented 70% of the population (Watson 1986), and of the interactions involving adult and non-adult birds, 94% were initiated by adults. Male and female adults were equally common in the study area (Watson 1986) and initiated aggressive displays with similar frequencies ($\chi^2 = 0{,}02$; $df = 2$; $p > 0{,}1$) regardless of the stage of the breeding cycle (Table 1). Of the displays directed at other adults, significantly more of them ($\chi^2 = 10{,}8$; $df = 3$; $p < 0{,}01$) were directed at birds of the same sex (Table 2) than at individuals of the opposite sex.

**Table 1** The number of intraspecific aggressive displays seen during ad-libitum sampling (1981–1984), in the incubation, nestling and post-fledging stages of the breeding cycle

| Nesting stage and Defender | | Aggressive displays initiated by: Adult ♂ | Adult ♀ | Non-adult ♂ | Non-adult ♀ | Sex unknown (U) |
|---|---|---|---|---|---|---|
| **Incubation** | | | | | | |
| Adult | ♂ | 4 | 1 | 1 | 2 | 1 |
| Adult | ♀ | 2 | 6 | 0 | 0 | 0 |
| Non-adult | ♂ | 5 | 6 | 1 | 1 | 0 |
| Non-adult | ♀ | 8 | 4 | 1 | 1 | 0 |
| Non-adult | U | 16 | 11 | 2 | 1 | 1 |
| **Nestling** | | | | | | |
| Adult | ♂ | 8 | 3 | 1 | 0 | 0 |
| Adult | ♀ | 1 | 8 | 0 | 0 | 0 |
| Non-adult | ♂ | 6 | 0 | 0 | 1 | 0 |
| Non-adult | ♀ | 6 | 11 | 1 | 0 | 0 |
| Non-adult | U | 16 | 9 | 2 | 0 | 2 |
| **Post-fledging** | | | | | | |
| Adult | ♂ | 2 | 2 | 0 | 0 | 1 |
| Adult | ♀ | 1 | 3 | 0 | 1 | 0 |
| Non-adult | ♂ | 3 | 2 | 0 | 0 | 0 |
| Non-adult | ♀ | 4 | 4 | 0 | 0 | 1 |
| Non-adult | U | 6 | 2 | 0 | 1 | 2 |
| **Total** | | 88 | 72 | 9 | 8 | 8 |

Rates of aggressive display (number of displays per individual of each age class per month during a particular stage of the breeding cycle) were used to compare the intensity of aggression towards adults and non-adults, and between stages of the breeding cycle (Figure 1). Adults displayed to other adults less often ($p < 0{,}001$; Mann-Whitney $U = 95$; $n_1 = 10$; $n_2 = 10$) than to non-

**Table 2** The number of aggressive displays initiated and received by resident bateleurs during focal-bird observations

| | Number of aggressive displays | | | |
|---|---|---|---|---|
| | initiated by resident | | received by resident | |
| Non-resident | Male | Female | Male | Female |
| Adult ♂ | 2 | 0 | 1 | 0 |
| Adult ♀ | 0 | 6 | 0 | 1 |
| Non-adults | 42 | 27 | 3 | 1 |
| Age class not identified | 8 | 16 | 2 | 2 |
| Total | 52 | 49 | 6 | 4 |

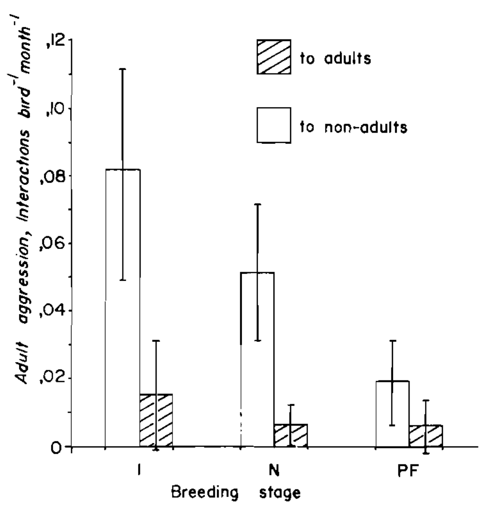

**Figure 1** Mean (and *SD*) adult aggression towards other adult and non-adult bateleurs at different stages of the breeding cycle. I = Incubation, N = Nestling, PF = Post-fledging periods. Data from ad-libitum sampling from June 1981 to September 1984. Breeding stage was taken as the population average for each year respectively (Watson 1986), and mean (*SD*) values were calculated between years.

adult birds. The rate of interaction between adults remained fairly constant throughout the breeding cycle, while the rate of interaction with non-adults decreased significantly (Kruskall-Wallis H = 5,6; $df = 2$; $p < 0,05$) from the incubation stage to the post-fledging stage (Figure 1).

The number of displays initiated by non-adults was low (Table 1). Because non-adult aggression did not appear related to any environmental condition at the time that it was performed, I considered it to be a 'play' behaviour (Wallace 1979).

Resident birds, observed during focal-bird sampling, initiated significantly more aggressive displays ($\chi^2 = 74,6$; $df = 1$; $p < 0,001$) than non-resident birds (Table 2). The majority (90%) of the 77 aggressive displays initiated by resident birds were directed towards non-adult bateleurs. The rest were directed at adults of the same sex (Table 2); none were directed at adults of the opposite sex. Male and female resident birds initiated displays with equal frequency ($\chi^2 = 0,05$; $df = 1$; $p > 0,8$). Two of the displays initiated by non-resident birds were by adults of the same sex as the defending resident bird, while the rest were initiated by non-adults (Table 2). No displays were initiated by adults of the opposite sex of the residents.

The mean distance away from the nest site at which displays were initiated by resident birds was 1,9 km, but few displays were initiated within 1 km of the nest (Figure 2). When compared with the bateleur's usually unimodal pattern of home range use centred close to the nest site (Watson 1986), the fact that most displays occurred more than 1 km from the nest site (Figure 2) suggests that resident birds actively approached non-residents as the latter approached the nest site.

The presumed function of territorial aggression is to drive intruders away from the territory centre or nest site. In 68 displays where the resident bird's initial and final positions were known, it was found that they had moved closer to the nest (30 of 68 cases) as often as moved away from it (30 of 68 cases) when they broke off the display. The mean change in distance from the nest was only 0,01 km, effectively no change at all. Resident birds increased height (31 of 68 cases) as often as maintained height (31 of 68 cases) but rarely decreased height ($n = 6$). However, intruders increased height (53 of 68 cases) significantly more often ($\chi^2 = 7,96$; $df = 1$; $p < 0,01$) than they remained at the same height or decreased height. Thus, the response by the intruder was usually to retreat by gaining height, resulting in the resident bird 'winning' the interaction, regardless of the horizontal distance from the nest.

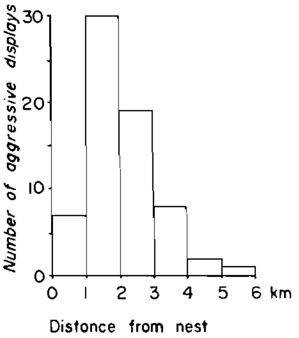

**Figure 2** Frequency distribution of distances from the nest at which aggressive displays were initiated by resident focal bateleurs.

Aggression by bateleurs continued throughout the year, and territories were maintained even during the non-breeding period (Table 3). In addition, territories were maintained in non-breeding years (pair B) and after a July breeding failure (pair A).

The intensity of aggression was measured by the number of aggressive displays per encounter with intruding birds (I/E, Figure 3) instead of the number of aggressive displays towards intruding birds per hour (I/h, Figure 3). This was done because the number of non-adults in the population varied (Watson 1986), so the rate of encounters with intruding birds (E/h, Figure 3) also varied. Although the encounter rate (E/h) varied significantly through the year ($\chi^2 = 72,5$; $df = 10$; $p < 0,001$), the interaction rate (I/h) tracked the variations quite closely. Thus, there was no significant variation ($\chi^2 = 5,6$; $df = 10$; $p > 0,05$) in the intensity of aggression, I/E, through the year (Figure 3). The latter observation, made on a few known pairs of bateleurs, contrasts with the progressive decrease in the interaction rate between incubation and post-fledging stages apparent from instantaneous sampling (Figure 1), and may be the result of inter-pair differences in the stage of breeding in any given month. It can be concluded that aggression is maintained throughout the year, including non-breeding periods, by specific pairs. In general, however, there may be a trend for aggression

**Table 3** The number of aggressive displays initiated by resident bateleurs and their breeding status at the time for each month of 1983

| | Breeding status and number of aggressive displays | | | |
|---|---|---|---|---|
| Month | Pair A | Pair B | Pair C | Pair D |
| Jan | NB/2 | NB/0 | I/0 | ?/0 |
| Feb | I/NA | NB/NA | I/NA | ?/NA |
| Mar | I/6 | NB/0 | N/0 | I/1 |
| Apr | N/5 | ND/2 | N/8 | ?/4 |
| May | N/0 | NB/2 | N/0 | ?/6 |
| Jun | N/5 | NB/1 | N/0 | I/0 |
| Jul | N/3 | ND/4 | PF/1 | I/0 |
| Aug | NB/1 | NB/3 | PF/4 | N/0 |
| Sep | NB/2 | NB/3 | PF/2 | N/2 |
| Oct | ND/1 | ND/3 | PF/4 | N/3 |
| Nov | NB/7 | ND/3 | ND/1 | N/4 |
| Dec | NB/0 | NB/0 | NB/11 | PF/5 |
| Total | 32 | 21 | 31 | 25 |

NB = Non-breeding, I = Incubation period, N = Nestling period, PF = Post-fledging dependence period, ? = Status unknown. NA =Not applicable because no focal sampling observations were made in this month.

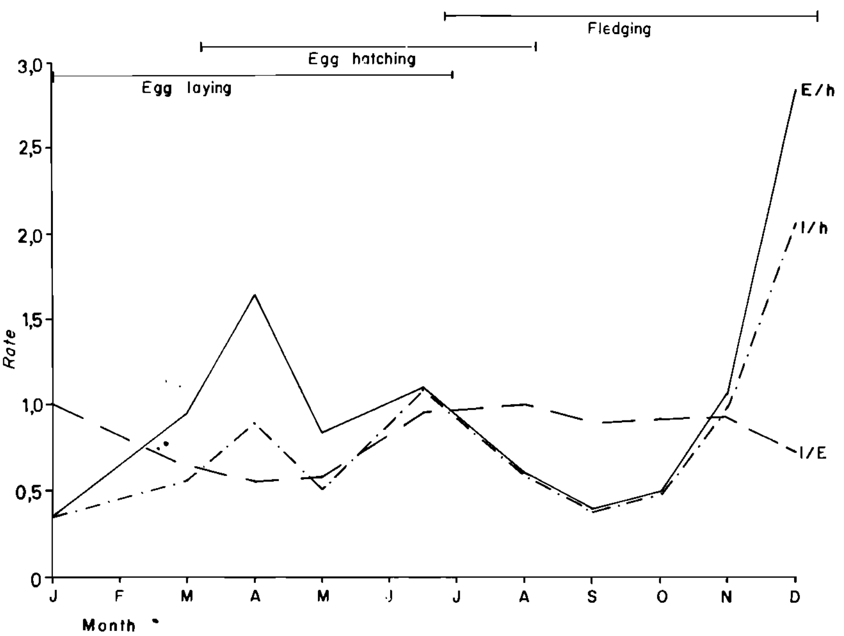

**Figure 3** Variation of the intensity of aggression (I/E) in relation to time of year and breeding stage. The egg-laying, egg-hatching and fledging periods are derived from Watson (1986). Interaction data are from 172 h of focal-bird observations, including 109 incidences of aggression and 39 encounters without aggression. E/h = Number of encounters per hour, I/h = Number of aggressive interactions per hour, I/E = Number of aggressive interactions per encounter.

to be most intense in the early stages of the breeding year, decreasing progressively thereafter.

## Discussion

In general, territorial aggression is defined as involving at least occasional attacks on intruders, and displays that are initiated mainly by adults and directed at adults of the same sex (Manning 1972; Wallace 1979). The results show that the bateleurs' aggressive display fits this general definition, and that it was used by adults in 50 – 100% of encounters with intruders (Figure 3) to defend a territory around the nest site. On average, territory holders did not shift position during a display to an intruder, suggesting that the mere presence of the territory holder in the vicinity of the intruder was enough to ward it off. Bateleurs attacked by a territory holder always submitted, usually by retreating to a higher altitude. The existence of an upper boundary to the territory has also been found in other raptors (Craighead & Craighead 1969), such as the black eagle *Aquila verreauxi* (Gargett 1975) and African fish eagle *Haliaaetus vocifer* (Brown 1980). Submissive retreat from an aggressive display is typical of territorial displays, where the context of the display is important (Maynard Smith & Parker 1976; Davies 1978). This may be expected with predators in which the risk of injury to an intruder influences its response to the resident.

Davies & Houston (1984) noted that the existence of territoriality depended on resource quality and distribution in space and time, and potential competition for the resource. The resources are usually considered to be food or mates, although others, such as nest sites, may also be important. Both sexes of a pair of bateleurs aggressively defended their territory and new pair formation, when competition for mates is most intense, is rare in this long-lived species that probably pairs for life (Watson 1986). Therefore, unless the mates are defending their investment in each other, they are not likely to be the main resource defended by territorial pairs. The existence of an altitudinal territory limit suggests that a gain in height reduces the intruder's ability to use the limited resource. This observation indicates that food may be the disputed resource because a gain in height should reduce the intruder's ability to forage over the territory holder's range. The principal benefit of territoriality may change depending on the stage of the breeding cycle. For example, territorial aggression in non-breeding years shows long-term maintenance of territories, which implies that protection of time or energy investments (e.g. familiarity with food distribution) may be involved as benefits from territory maintenance.

Territorial aggression was shown by resident bateleurs mainly towards non-adults, suggesting that young birds may be a greater competitive threat to the resident territory holder than other adults. Non-adults may be greater competitors for food because of their greater mobility relative to nesting adults. Alternatively, non-adults way be more likely to attempt a territory take-over than other adults which may already be established or, because non-adults are nomadic (Watson 1986) they are more likely to enter an occupied territory by accident.

The few adults that elicited aggressive displays were the same sex as the territory holder, as predicted of territorial aggression (Wallace 1979). That relatively few aggressive encounters occurred between adults, as found in other raptors, such as black eagles (Gargett 1975), and ospreys *Pandion haliaetus* (Jamieson & Seymour 1983), possibly results from habituation to individually recognized neighbours, as found in songbirds (Falls & Brooks 1975). The lack of aggressive displays between adults also suggests a low incidence of non-territorial roaming adults.

Instantaneous sampling indicated that the intensity of aggression by adults towards non-adults changed through the breeding season and, therefore, could have a seasonal effect on the local movements, distribution and abundance of non-adults. As such, adult aggression over several seasons may encourage dispersal from natal sites in this species which has a seven to eight year non-adult development period (Brown & Cade 1972).

Aggression by non-adults represented 15% of the total number of aggressive displays seen. It was not studied in detail because individual birds could not be recognized and non-adults were highly mobile, not remaining in any one locality for long. Non-adult aggression, considered to be 'play' behaviour, seemed to have no obvious function in determining the distribution of individuals. However, play can be expected in animals in which learning and social interactions are important (Wallace 1979). It is thought to be adaptive because it familiarizes young animals with their surroundings and develops their ability to deal with any social or potentially hazardous situations that may arise.

The aggressive display of the bateleur is seen in all stages of the breeding cycle, including non-breeding periods, and it fulfills the definition of territorial aggression. Territoriality is ecologically significant because, as in other raptors (Newton 1979), it is probably the proximate factor limiting bateleur densities in suitable habitat. Bateleur territory size, shape and stability may conform to the predictions of one or more territory models (Schoener 1983), as demonstrated for other raptors (Newton 1976; Janes 1984), and the spatial properties of territorial behaviour may predictably affect its population dynamics (Jones & Krummel 1985). Aggression and territoriality probably also affect the movements and distribution of non-adult bateleurs.

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