The consequences of crowned eagle central-place foraging on predation risk in monkeys

Susanne Shultz^{1,2*} and Ronald Noë^{2,3,4}

¹Population and Evolutionary Biology Research Group, School of Biology, Nicholson Building, University of Liverpool, Liverpool L69 3GS, UK

²Taï Monkey Project, Centre Suisse des Recherches Scientifiques, 01 BP 1303 Abidjan 01, Ivory Coast

³Ethologie et Ecologie Comportementale des Primates, Université Louis Pasteur, F-67000 Strasbourg, France

⁴Max-Planck Institut Seeewiesen, D-82305 Starnberg, Germany

The African crowned eagle (*Stephanoaetus coronatus*) is the primary predator for arboreal primates throughout sub-Saharan forests. Monkeys typically respond with alarm calls when they are aware of the presence of crowned eagles and such calls can be considered a corollary of predation risk within primate groups. Alarm calls from six species of monkeys were recorded across the home range of an eagle pair in Taï National Park, Côte d'Ivoire. Spatial and temporal variation in primate alarm calling was found to be related to eagle ranging behaviour according to the predictions of central-place foraging models. Radio-tracking data indicate that eagle activity is higher in the centre of their home range and monkey alarm-calling rates are correspondingly elevated near eagle nests as opposed to farther away. Alarm-calling rates are also temporally coupled with measures of eagle activity. There were considerable differences between the species in both rates and spatial patterns of alarm calling. The variation we measure in predation risk is expected to have consequences at the behavioural and population level.

Keywords: anti-predation behaviour; predator foraging; alarm calling; prey encounter rates

1. INTRODUCTION

Most investigations of predator–prey systems generally invoke a variation of the Lotka–Volterra model, where the predation rate serves as the principal limiting factor in prey population abundance. In many systems it is also necessary to consider the non-lethal effects in predator–prey interactions. The extreme fitness costs incurred by a successful predation event can drive the evolution and maintenance of elaborate and expensive anti-predation behaviours, leading to potential trade-offs between predation and anti-predator behaviour. Although individuals can respond to increases in predation risk by changes in habitat use, grouping patterns, time budgets and resource allocation (reviewed in Lima 1998), they have little control over predation risk and the resulting stress and investment necessary to counteract predator strategies. Predator-induced stress has been found to decrease snowshoe hare reproductive rates (Hik 1995) as well as lower growth rates in a variety of other species (Lima 1998). Thus, increased predation risk, even in the absence of increased predation rate, can cause reductions in prey fitness via the effects of higher stress levels or changes in energy budgets caused by behavioural responses. One straightforward way of estimating predation risk is to measure the predator–prey encounter rate. An increase in the frequency of encounters with predators can have two consequences: prey individuals must either invest more in defence or accept a higher level of risk. The actual predation rate depends on the efficacy of the anti-predator strategy employed and the level of investment in it.

Previous attempts to document the impact of predation

risk on resource allocation and anti-predator behaviour in natural populations have concentrated on comparisons between communities with different predator densities (e.g. Van Schaik & Van Noordwijk 1985; Heard 1992). The main deficiency in this approach is that it is difficult to control for underlying ecological differences between habitats. Small differences in productivity, resource availability or habitat structure can manifest themselves through non-intuitive ecological responses within the prey community (Janson 1998). A better test of the effects of predation risk on prey behaviour is to use a natural experiment and observe individuals from the same population that are exposed to different levels of predation risk.

Where predators unevenly exploit prey populations either over space or over time, it should be possible to document the effects of variable predation risk on the prey population. One such example where predator behaviour can have a spatial impact on predation risk is with central-place foragers (CPFs). CPFs are expected to depress resources unevenly across their home range because of the high cost of prey transport to the nest or den (Orians & Pearson 1979). Even if direct exploitation does not change the prey density, exposure to predators can result in a reduced capture rate or depressed prey *availability*, if prey employ behavioural evasion such as increasing vigilance levels or retreating to refuges after encounters (Charnov *et al.* 1976). CPF predators that repeatedly return to a nest will necessarily encounter prey near the central place more often than prey on the periphery of their range. Unless prey can accurately determine whether a predator is foraging or not, they will treat all predator encounters as potential predation events and employ a risk-averse strategy using relevant anti-predator behaviours. Central-place foraging models have been widely applied to raptors (e.g. Andersson 1978; Korpimäki *et al.* 1994). In nesting

*Author for correspondence (smshultz@liverpool.ac.uk).

Table 1. The results of alarm-calling rates for six diurnal monkey species in Taï National Park. (The densities were estimated from the Taï Monkey Project (Höner 1993; Wachter *et al.* 1997). The body size data come from Oates *et al.* (1990). Figures for the total calls in parentheses represent the total calls before exclusion for non-independence.)

species	body size (g)	population density (individuals km ⁻²)	approximate home-range size (ha)	total calls	calls (h ⁻¹)
<i>C. diana</i>	3900	75	62	192 (292)	0.396
<i>C. campbelli</i>	2700	30	50	50 (97)	0.103
<i>C. petaurista</i>	2900	20	100	6 (15)	0.012
<i>P. badius</i>	8200	155	57	29 (36)	0.060
<i>C. polykomos</i>	8300	45	55	32 (70)	0.066
<i>C. verus</i>	3950	15	62	—	—
<i>C. atys</i>	6200	25	500	23 (40)	0.047

species with a protracted dependency period of offspring, parents may behave as CPFs for most of the year.

This study tests the spatial implications of central-place foraging on predation risk in a natural system comprising primate prey in the home range of a significant primate predator, the African crowned eagle (*Stephanoaetus coronatus*), using alarm calls as a measure of predator encounter rates. Crowned eagles provide an ideal test case for models of spatial variation in predation risk. They defend evenly spaced territories, provision brooding parents or young for 18 months of each 24 month reproductive cycle (Brown *et al.* 1982), thus fulfilling the assumptions for CPF models (see Orians & Pearson 1979; Nilsson *et al.* 1982; Korpimaki *et al.* 1994). Crowned eagle prey consists of medium-sized mammals, with primates making up most of the prey in Taï National Park (Shultz 2002). The monkeys in Taï have considerably smaller home ranges than the eagles (0.5–5 km² versus 6.5 km², see table 1). As the habitat is covered by monkey group home ranges, some monkey groups will be near eagle nests, while others will be near the periphery of eagle territories.

Our first objective in this study was to document the spatial patterns of primate predation risk in relation to the distance from the nest of an African crowned eagle. To determine whether there was variation in perceived risk, we measured alarm-calling rates at different distances from the eagles' nest. Alarm calls are a typical response of social primates to predators, and previous studies have shown that alarm calls can be elicited by simulating encounters with crowned eagles (e.g. Zuberbühler *et al.* 1997). Our second objective was to compare spatial and temporal patterns of monkey alarm calling with eagle ranging and activity patterns. We predict that if eagles are important monkey predators, alarm-calling rates should be elevated in areas intensely used by eagles and during periods of heightened eagle activity. Finally, we relate the species differences in alarm-calling behaviour to ecological characteristics. We suggest that those species that are more vulnerable should more reliably respond to eagle encounters and monkey groups located near the centre of eagle territories should show behavioural responses to heightened risk levels.

Figure 1. Crowned eagle nest sites and distribution of listening posts across a crowned-eagle home range. The scale is approximate. Black stars, nest sites monitored for eagle activity; black squares, nests; white circles, recording sites; white pluses, research camps; lines, trails. The inset shows the focal eagle home range and recording locations.

2. MATERIAL AND METHODS

(a) Study site

Taï National Park is located in southwestern Côte d'Ivoire and is the largest (454 000 ha) continuous primary tropical moist forest in West Africa. Eight monkey species are found within the study area: Diana monkey (*Cercopithecus diana*), Campbell's monkey (*Cercopithecus campbelli*), lesser spot-nosed monkey (*Cercopithecus petaurista*), putty-nosed monkey (*Cercopithecus nictitans*), sooty mangabey (*Cercocebus atys*), Western red colobus (*Procolobus badius*), Western black and white colobus (*Colobus polykomos*) and the olive colobus (*Procolobus verus*). There are four major predators of monkeys in Taï: crowned eagles, leopards (*Panthera pardus*), chimpanzees (*Pan troglodytes*) and humans. All work was carried out at the Centre de Recherche en Ecologie research station in the Taï National Park ca. 20 km southeast of the town of Taï. The data presented stem from groups habituated to the presence of observers as well as unhabituated groups. Noë & Bshary (1997), Zuberbühler *et al.* (1997) and McGraw (1998) provide more information on the study site, polyspecific associations and alarm-calling behaviour of the monkey species found in Taï.

(b) Alarm-call recording

Data were collected by S.S. and R. N. S. Kami from December 1998 to July 2000. Nine sampling locations, which were evenly distributed across the estimated home range of one crowned eagle pair (figure 1), were selected (one site in the

range centre, four sites 650 m from the nest and four sites 1250 m from the nest). All recording sites were located a minimum of 1500 m from other known eagle nests. At the beginning of the study, the pair were provisioning an older dependent offspring, they began a second nesting cycle and eventually fledged, but continued to provision a second offspring towards the end of the study period. As crowned eagles are territorial (Brown 1976), the target home range was estimated by assuming non-overlapping territories with neighbouring eagle pairs. Ranging data collected on radio-tagged eagles supported this assumption. Data were recorded for 45 min in each location and the locations were visited in a random order. The first recording session began between 07.00 and 07.30 and the final recording session began between 16.30 and 17.00. On average just over eight of the nine sites were visited on any given day. The total recording time was 486 h (ca. 54 h per site) over 80 days. At each location, the audible or visible presence of any monkey species was noted every 20 min to provide a relative index of monkey activity at each sampling location as an indirect measure of monkey abundance. Audible presence was based on species-typical intra-group vocalizations.

Alarm calls were recorded from all species except *P. verus* and *C. nictitans*. The loud calls of the male *C. diana*, *C. campbelli*, *C. petaurista*, the loud yells of *C. atys*, the 'ow' call of *P. badius*, and the roaring of the male *C. polykomos* were counted as alarm calls. These calls have previously been recorded during predator encounters by Tai Monkey Project observers. For each alarm call, the following information was recorded: time, compass direction from the listening post, duration of the calling bout, estimated distance from the observer (recorded into categories of 0–50 m, 50–100 m, 100–250 m and 250–400 m), and the observer confidence in call direction and distance (1–5 scale from low to high confidence). Low confidence scores were given to calls given by distant groups or by overlapping calls whereby the more distant group was difficult to localize. Each call was then located on a map of the eagles' home range using the estimated direction and distance from the known listening posts. Calls were grouped into 125 m distance classes from the nest site. Any calls given within 10 min of a previous call of any species, or that were located closer to another eagle nest, were discarded as non-independent. The stimulus causing the alarm was recorded when known; stimuli included predators heard or seen, falling branches, allospecific and conspecific alarm calls and calls directed at the observer or other humans. We only had a single recording location close to the nest as compared with four locations each at intermediate and far distances. We calculated call rates for each distance class by dividing the total number of calls heard at each distance by the total time we recorded at that distance.

The total alarm-calling rate for all species in each distance class was regressed against distance from the eagles' nest, and alarm-calling rates over time were correlated with measures of eagle activity. Separate regression analyses of call rate against distance from the eagles' nest were carried out for the three different call stimuli categories:

- (i) calls known to be given to eagles;
- (ii) calls for other known stimuli; and
- (iii) calls given for unknown reasons.

For species-by-species analysis, all alarm calls were used, whether or not the stimuli were recorded, as too few calls given

to specific stimuli were recorded to allow for separate analysis by monkey species.

(c) *Measure of eagle activity and ranging behaviour*

Two adult female eagles, with dependent young, were captured and fitted with tail-mounted radio transmitters with activity sensors. Eagle locations were taken by following a randomly chosen course on systematic transects across an area larger than the estimated home range of an eagle pair. Once found, eagles were followed as long as possible with activity and locations recorded at 10 min intervals. The location of the eagles was determined by triangulation, an initial location was followed by a second location 50 m along the transect and approximate location was later determined. Hourly locations were used in determining eagle-ranging behaviour in order to minimize the effects of non-independence.

Six known crowned eagle nests were monitored at least one day per month between December 1998 and December 1999. For each observation day, an observer (S.S. or R. N. S. Kami) remained at the nest site from 07.00 to 17.00 and recorded when eagles were seen on or near the nest, eagles leaving or arriving at the nest and eagle calls heard throughout the day. Adult eagles arriving and leaving the nest site and eagles heard were counted in the activity index (no. of eagle records per hour). Different eagle pairs have asynchronous reproductive cycles; pooled activity patterns over all nests provide an average index of the eagle-activity patterns.

3. RESULTS

(a) *Alarm calls and monkey-activity patterns*

During the observation period 611 total alarm calls were recorded; 61 recorded calling events with low observer confidence (score of 1) were excluded *a priori* from the analysis. Of the 550 recorded calls remaining, 227 calls were removed from the analysis because either non-independence (158) or calls were located closer to a second nest rather than the focal nest (69). Of calls given in response to a known stimulus, 29 (5.3%) were given immediately after an eagle was seen or heard by the observer, six (1.1%) were given in response to nearby chimpanzees, four (0.7%) were given in obvious response to the observer, two (0.3%) in response to gun shots, seven (2.2%) in response to falling branches heard and 133 (24%) were given immediately following a call from another species. Over 66% of the alarm calls were given in response to a stimuli neither seen nor heard by the observer. The recorded stimuli had an unequal likelihood of causing multiple alarm calls from different species ($\chi^2 = 11.6$, d.f. = 5, $p = 0.04$); 48% of calls given in response to eagles, 25% of calls given in response to observers and 100% of calls following gun shots were followed by a second call of another group, while multiple calls were not evoked by other stimuli. The likelihood for giving an alarm call following the alarm call of a previous group differs significantly between species ($\chi^2 = 14.03$, d.f. = 5, $p = 0.015$; figure 2). However, removing calls from Diana monkeys from the analysis resulted in no significant difference between the species ($\chi^2 = 7.16$, d.f. = 4, $p = 0.128$). A summary of primate density estimates, home-range sizes, calling frequencies and rates can be found in table 1. Neither body size nor population density

Figure 2. Observed and expected frequencies of alarm calls given following the calls of another group for all species. The empty and shaded bars represent the actual and expected values, respectively.

Figure 3. The temporal relationship between eagle activity and primate alarm calls. Eagle activity (circles) was measured as arrivals and departures from a nest site. The alarm calls (squares) were compiled for all species from all alarm-recording sites.

are correlated with calling rates (body size, $r^2 = 0.06$, $n = 6$, $p = 0.31$; density, $r^2 = 0.03$, $n = 6$, $p = 0.365$). The index of monkey activity did not show any spatial trend with increasing distance from the eagle nest (ANOVA, $F_{1,7} = 0.01$, $p > 0.9$).

(b) Eagle ranging and activity

The data for the eagle-activity patterns were generated from observations of six eagle nests and are independent from the measures of both eagle ranging and monkey alarm calling. The total observation time was 312 h over 26 days distributed approximately evenly over the six nest sites. Eagle ranging behaviour was based on 61-point locations collected over 20 days of observation. The recorded eagle activity was greater in the morning than in the afternoon ($t = 3.59$, d.f. = 6, $p = 0.01$; figure 3). There was a significant negative relationship between the fre-

Figure 4. Eagle location frequency (circles) and alarm-calling rates (squares) for six diurnal primates as a function of distance from a crowned hawk-eagle nest site. Each point represents either the overall call rate or the number of times an eagle was located in each 125 m class.

Table 2. The regression analyses of alarm-calling frequency against log distance from eagle nests.

species	<i>F</i>	d.f.	<i>r</i> ²	<i>p</i>
<i>C. diana</i>	33.12	1,12	0.73	< 0.001
<i>C. campbelli</i>	29.15	1,12	0.71	< 0.001
<i>C. petaurista</i>	3.15	1,12	0.21	0.10
<i>P. badius</i>	1.62	1,12	0.12	0.23
<i>C. polykomos</i>	4.72	1,12	0.28	0.05
<i>C. atys</i>	0.43	1,12	0.04	0.53

quency of the eagle locations and the distance from the eagle nest ($F_{1,12} = 10.68$, $p < 0.01$; figure 4).

(c) Spatial and temporal variation in primate alarm calling

The monkey alarm-calling rates over all species declined significantly with increasing distance from the eagle nest ($r^2 = 0.73$, $F_{1,12} = 32.74$, $p < 0.001$; figure 4). This relationship held even when calls closer to a second nest were included in the analysis ($r^2 = 0.67$, $F_{1,12} = 26.3$, $p < 0.001$). Alarm calls known to be given to eagle stimuli showed the same pattern ($n = 28$, $r^2 = 0.56$, $F_{1,12} = 15.29$, $p = 0.002$ before removing non-independent calls; $n = 15$, $r^2 = 0.45$, $F_{1,12} = 9.70$, $p = 0.009$ after removal), whereas calls given to other identified stimuli did not show a trend with distance from the eagles' nest ($n = 24$, $r^2 = 0.063$, $F_{1,12} = 0.81$, $p = 0.39$ before removal of calls; $n = 18$, $r^2 = 0.009$, $F_{1,12} = 0.110$, $p = 0.745$ after removal). The alarm-calling rates were significantly correlated with the frequencies of the eagle locations ($r^2 = 0.47$, $n = 14$, $p < 0.001$), both declining with distance away from the eagle nest. The rate of alarm calling was significantly correlated to the activity pattern of the eagles ($r^2 = 0.35$, $n = 9$, $p = 0.047$; figure 3). This relationship remains significant for three of the six monkey species when examined individually, while the same trend remains for an additional two species (table 2). If distance classes with zero values are excluded for red colobus, then the relationship is also significant ($r^2 = 0.546$, $F_{1,12} = 7.21$, $p = 0.036$).

4. DISCUSSION

Until now, evidence of spatial variation in predation risk has centred more on microhabitat use by prey individuals and less on the foraging and ranging behaviour of predators (Cowlshaw 1997; Lima 1998). The strong relationship between eagle foraging patterns and monkey alarm-calling rates documented here indicates that prey experience variable levels of predation risk depending on their position within a predator's range. Where individuals or groups of prey hold stable home ranges that saturate the available habitat, some individuals may not have access to low-risk areas. As we gain a better understanding of how predators exploit resources over space, we can use this knowledge to understand the effects of relative predation risk at the population level. A logical continuation of the findings presented here would be to look for behavioural variation over a gradient of predation risk. We expect individuals under heightened risk to modify their behaviour in order to ameliorate risk. They may forage in less exposed locations, allocate more energy and time to vigilance behaviours, spend more time in polyspecific associations or show more group cohesion than individuals under lower risk levels. The effect is expected to vary between species depending on their location in the canopy while foraging and their resultant exposure to eagle attacks.

Our results are largely inferred because the exact stimulus is unknown for all calls. However, spatial and temporal patterns expected from alternative sources of alarm-calling stimuli clearly are not supported by the data. If alarm calls are directed at other predators or function more often for inter-group communication, we would expect no spatial or temporal relationship between eagle-activity patterns or range use. As we have shown a strong relationship between both of these variables and monkey alarm-calling rates, eagle behaviour is directly implicated in eliciting the monkey alarm calls. Additionally, call rates given to eagles show a consistent decline with distance from the nest, whereas calls given to other known stimuli do not show this spatial pattern. The limited amount of ranging data available for these eagles indicates that they do function as CPFs. Additional ranging data from other eagle individuals, especially adult males, may better clarify the general patterns of range use over territories and over an entire reproductive cycle. The distribution of recording locations is not associated with the known home ranges of either leopards or chimpanzees and there is no indication from previous work that either species uses the area around the crowned eagle nest disproportionately (leopards, Jenny 1996; chimpanzees, Herbinger *et al.* 2001). Furthermore, the population density of leopards is much lower than that of eagles (Shultz 2002), resulting in lower encounter rates between them and specific monkey groups.

The monkey species in Tai demonstrate obvious differences in alarm-calling behaviour. Due to the strong spatial relationship with the distance from the eagle nests, the results support previous evidence that Diana and Campbell's monkeys have distinct calls for aerial predators (Zuberbühler 2000), and it is likely that the polykomos loud calls are also given in response to the detection of aerial predators. As neither body size nor population density is correlated with alarm-calling rates, the variation in calling rates between species is evidence of distinct anti-

predator behaviour and variation in risk levels caused by ecological and behavioural differences in canopy use, group cohesion, group composition and time in polyspecific associations. Three of the species, the Diana monkey, lesser spot-nosed monkey and Campbell's monkey live in single male groups; black and white colobus occur in single male or small multi-male groups, while mangabeys and red colobus occur live in large multi-male groups. Of all the species, the Diana monkey and red colobus forage in the highest levels of the canopy (McGraw 1998) and therefore can be expected to experience higher levels of predation risk by eagles than other species. Diana monkeys have the highest calling rate and are the most reliable sentinels (Bshary & Noë 1997). Both of these species gave more alarms without hearing a previous alarm of another group than the other four species; after removing Diana monkeys from the analysis the other species did not differ in their likelihood to give calls in response to other groups.

These findings may indicate that the vigilance of Diana monkeys is exploited by other groups that are less likely to detect eagles. Alarm calling may indicate to a passing eagle that it has been detected and may have a higher capture rate success by moving on to more unwary groups. Observations of hunting eagles indicate that the eagles use a sit-and-wait strategy, waiting for monkey groups to move into exposed locations in the canopy before attacking (Shultz 2001). Leopards, like eagles, are ambush predators that rely on surprise. Playbacks of monkey alarm calls have been shown to cause leopards to move away from a nearby monkey group sooner than expected without an alarm call being given (Zuberbühler *et al.* 1999). The frequent polyspecific associations in Tai may be a result of the more cryptic species (e.g. olive colobus) or less-exposed (e.g. Campbell's and lesser spot-nosed monkeys) using Diana monkeys as a 'watchdog'. Previous observations indicate that all species except the mangabey and black and white colobus spend much of their time in association with a Diana monkey group (Höner *et al.* 1997; Noë & Bshary 1997).

Several possible reasons may explain the lack of a significant relationship between alarm-calling rates and the distance from the eagle nest in three of the species. One possible reason for the lack of spatial pattern is that the vocal repertoire of these species may lack a call used exclusively for aerial predators. Additionally, communication has only been well studied in two of the species, the Diana monkey and Campbell's monkey, and we are confident about which calls are used in an alarm context. Lack of understanding of the vocal repertoires of other species may have resulted in classifying non-relevant calls as alarms. Furthermore, red colobus do not have a 'loud' call that travels as far as the male calls of Diana monkeys, Campbell's monkeys and black and white colobus. For this reason, the recorded alarm rates may be underestimates of the actual alarm-calling rates within groups and may have resulted in distance classes with no recorded alarms. When these values were eliminated, red colobus also showed a decline in calling rate with distance to the nest. Mangabeys are the only terrestrial species in the forest, which heightens their risk to predation by terrestrial predators. Although leopard diets in Tai include all monkey species, terrestrial species are taken more often than arboreal ones (Hoppe-Dominik 1984).

By using monkey alarm-calling rates as a proxy for predator encounters, we were able to demonstrate a variation in predation risk over the home range of a crowned eagle pair. This confirms a basic assumption about the effect of a CPF on its prey. The overall activity levels of the primates did not vary with distance to the nest and the calling rates were tightly coupled with both activity patterns and space use by the eagles, both implying that eagle encounters were responsible for the observed spatial pattern in alarm-calling rates. These findings pave the way for a test of more specific hypotheses about the influence of perceived risk on the behaviour of primates.

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