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THE RESPONSES OF BLACK-CASQUED HORNBILLS TO PREDATOR VOCALISATIONS AND PRIMATE ALARM CALLS

by

HUGO J. RAINEY[1)], **KLAUS ZUBERBÜHLER**[2,3,4)] **and PETER J.B. SLATER**[1,5)]
([1] School of Biology, Bute Medical Buildings, University of St Andrews, St Andrews KY16 9TS, UK; [2] School of Psychology, University of St Andrews, St Andrews KY16 9JP, UK; [3] Centre Suisse de Recherches Scientifiques, Taï Monkey Project, Abidjan 01, Côte d'Ivoire)

Summary

Black-casqued hornbills (*Ceratogymna atrata*) forage in small flocks in the tropical forests of West Africa, often in the vicinity of primate groups, including Diana and Campbell's monkeys (*Cercopithecus diana*, *C. campbelli*). Previous work has shown that these monkey species produce acoustically distinct alarm calls to crowned eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*), two of their main predators. Black-casqued hornbills are highly vulnerable to crowned eagles, but not leopards, suggesting that individuals may respond differently to these two predators. We analysed the vocal response of these birds to field playbacks conducted on different monkey species in Tai National Park, Ivory Coast. We tested six stimuli, three of which related to the presence of a crowned eagle (eagle shrieks, Diana and Campbell's eagle alarm calls) and three to the presence of a leopard (leopard growls, Diana and Campbell's leopard alarm calls). Results showed that hornbills consistently distinguished between eagle- and leopard-related stimuli, suggesting that birds attended to the predator class associated with the various stimuli. Second, within eagle-related stimuli,

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[4)] Corresponding author's e-mail address: kz3@st-and.ac.uk

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hornbills responded more strongly to the actual predator vocalizations than the associated alarm calls. One interpretation of these data is that birds were sensitive to the precision of information concerning the location of the eagle. We discuss these results in light of previous data on hornbill behaviour and cognitive capacities.

Sommaire

Les réponses des grands calaos à casques noirs aux cris des prédateurs et aux cris d'alarme des primates. Les grands calaos à casques noirs *Ceratogymna atrata* se promènent en petit groupes dans les forêts tropicales d'Afrique de l'Ouest, souvent dans la zone dont grouille les groupes de primates, y compris le cercopithèque Diane *Cercopithecus diana* et le cercopithèque de Campbell *C. campbelli*. Des études précédentes révèlent que, devant leurs prédateurs — l'aigle couronné et la panthère — ces espèces de singes produisent des cris d'alarme distincts sur le plan acoustique. Les grands calaos à casques noirs sont hautement menacés par l'aigle couronné, et pas par la panthère, laissant supposer que les individus répondent différemment à ces deux prédateurs. Nous avons mené une série d'expériences d'enregistrements de terrain au Parc national de Taï, en Côte d'Ivoire, et avons mis à l'essai six différents *stimuli,* dont trois en rapport avec la présence de l'aigle couronné *Stephanoaetus coronatus* (le cris de l'aigle, les cris d'alarme du cercopithèque diane et du cercopithèque de Campbell) et dont trois en rapport avec la présence de la panthère *Panthera pardus* (les grognements de la panthère, les cris d'alarme du cercopithèque Diane et du cercopithèque de Campbell). Les résultats montrent que les calaos distinguent régulièrement les *stimuli* relatifs à l'aigle et à la panthère, laissant supposer que les oiseaux sont attentifs à la classe de prédateurs en rapport avec divers *stimuli.* Ensuite, dans les *stimuli* inhérents à l'aigle, les calaos ont répondu plus fortement à la voix réelle du prédateur qu'aux cris d'alarme y relatifs, laissant supposer qu'ils sont sensibles à la variation de l'information ainsi qu'à sa précision sur l'emplacement du prédateur. Nous discuterons de ces résultats à la lumière des données précédentes sur le comportement des calaos et leurs capacités cognitives.

Introduction

Various species of birds, rodents, carnivores, and primates produce acoustically distinct alarm calls to different classes of predators, or to the kinds of threats associated with them (*e.g.* Slobodchikoff *et al.*, 1991; Naguib *et al.*, 1999; Manser, 2001; Zuberbühler, 2003). In addition, some mammal species are able to discriminate between alarm calls of other species and to respond appropriately to them (*e.g.* Seyfarth *et al.*, 1980; Seyfarth & Cheney, 1990; Evans *et al.*, 1993; Oda & Masataka, 1996; Zuberbühler, 2000, 2001). A recent study has demonstrated that this ability is not restricted to mammals. Yellow-casqued hornbills *Ceratogymna elata* are vulnerable to predation by crowned eagles but not leopards. These birds distinguished appropriately between vocalisations of leopards, *Panthera pardus*, and crowned eagles, *Stephanoaetus coronatus*, as well as between the predator-specific alarm calls of sympatric Diana monkeys *Cercopithecus diana* (Rainey *et al.*, 2004). Eagle-related stimuli caused a significant increase in vocal behaviour and approach, but this was not observed for leopard-related stimuli.

The fact that hornbills behaved conspicuously in the presence of predatory eagles seems somewhat counterintuitive and requires further explanation. Conspicuous behaviour in the presence of a predator may be adaptive if it alerts nearby kin and other reproductively relevant conspecifics (Maynard Smith, 1965). This explanation may apply to mated pairs of hornbills that are often accompanied by their own offspring. However, solitary hornbills sometimes increased their call rates and approached the stimuli, implying that this behaviour is not solely directed at kin or conspecifics (Rainey *et al.*, 2004). A second line of argument suggests that conspicuous behaviour is adaptive if it negatively affects the predator's hunting behaviour, for example by signalling detection (Curio, 1978; Shelley & Blumstein, in press) and there is some empirical evidence suggesting that predators do respond to these signals (Tilson & Norton, 1981; Caro, 1995; Zuberbühler *et al.*, 1999). Detection signalling (or perception advertisement) could be an adaptive strategy in response to both eagles and leopards since both of them rely on surprising their prey (Zuberbühler *et al.*, 1999; Shultz, 2001). In the forests of Taï National Park, monkey alarm calls deterred leopards from hunting and caused them to leave the area, probably because of the lost element of surprise (Zuberbühler *et al.*, 1999). There is also some evidence that crowned eagles are deterred from hunting on hearing Diana monkey alarm calls (Shultz, 2001), suggesting that conspicuous vocal behaviour is an adaptive strategy in response to these predators. No systematic data are available for hornbills interacting with predators, although S. Shultz (pers. comm.) has made direct observations of hornbills approaching and calling to crowned eagles.

The ability to recognise and distinguish other species' alarm calls is clearly an adaptive trait as it provides individuals with information about the type of predator present without having seen it. Although monkey alarm calls have the capacity to encode information about predator type there is currently no evidence that these calls can encode information about the predator's spatial location (Zuberbühler, 2003). Not knowing the predator's whereabouts, however, might have important implications about the best anti-predator strategy to pursue. In particular, it might not be adaptive for individuals to engage in highly conspicuous behaviour until the predator is localised (Rainey *et al.*, 2004). There is evidence that some bird species produce alarm calls at a lower rate if they do not know the exact location of the predator (Curio, 1978; Conover, 1987; van der Veen, 2002).

Hypotheses and predictions

During field experiments on primates in Ivory Coast involving playback of predator calls and primate alarm calls, KZ found that hornbills were often in the vicinity of monkey groups. There was also some indication that they were calling in response to the stimuli and their calls were often tape-recorded concurrently with the primate calls. Accordingly, and in light of our findings in Rainey *et al.* (2004), we decided to assess the ability of hornbills to distinguish between different predator and primate calls. Black-casqued hornbills, *Ceratogymna atrata*, in Taï National Park live sympatrically with Diana monkeys, Campbell's monkeys, *C. campbelli*, crowned eagles, and leopards. They are amongst the largest forest birds (mass 0.9-1.6 kg, Kemp, 1995) in West Africa and, as such, are vulnerable to the same predators as the monkeys (Diana mass 2.2-7.5 kg, Campbell's mass 3-5.8 kg, Kingdon, 1997). Crowned eagles are known to prey on hornbills (Keith, 1969; Mitani *et al.*, 2001; Shultz, 2002). Leopards prey almost entirely on mammals, although bird remains have been found in their faeces (Hoppe-Dominik, 1984; Ray & Sunquist, 2001; Zuberbühler & Jenny, 2002). Leopards can climb up to the canopy where hornbills spend much of their time (Bshary & Noë, 1997), and hornbills may feed on the ground (HJR own data), but these are rare events.

Because of this and because of our previous results on yellow-casqued hornbills, we predicted that closely related black-casqued hornbills would increase the number of calls in response to eagle shrieks, but show little or no change in response to leopard growls. Both monkey species produce acoustically distinct alarm calls in response to crowned eagles and leopards (Zuberbühler *et al.*, 1997; Zuberbühler, 2000). Our second prediction therefore was that black-casqued hornbills would increase the number of calls in response to Diana eagle alarm calls, but show little or no change in response to leopard alarm calls. Third, the same response pattern was predicted when the birds were exposed to the alarm calls of Campbell's monkeys to these two predators (Zuberbühler, 2000). Finally, based on the previous considerations, we predicted that hornbills might produce higher rates of alarm calls in response to eagle shrieks compared to Diana or Campbell's monkey eagle alarm calls, due to the uncertainties concerning the predator's location in the latter two cases. However, we predicted no difference in call rates between their response to leopard growls and monkey leopard alarm calls.

Methods

Study site and species

KZ carried out the fieldwork between June 1994 and June 2002 in Taï National Park, Ivory Coast, in *ca* 100 km^2 of forest around the Centre de Recherche en Ecologie (CRE; 5°50′N, 7°21′W). Black-casqued hornbills are common throughout Taï but as canopy species they can be difficult to locate visually. It is difficult to provide an accurate estimate of abundance. For yellow-casqued hornbills, HJR encountered a group about every 5-8 km of transect walking, but black-casqued hornbills are about 50% more common (Rainey & Zuberbühler, subm.), suggesting an encounter rate of 1 group every 3-5 km of transect walking. In both species, local abundance varied strongly with season. Yellow- and black-casqued hornbills calls were ten times as abundant from July to February as they were from March to June (Rainey & Zuberbühler, subm.).

Black-casqued hornbills sometimes forage in small flocks in the vicinity of monkey groups, including Diana and Campbell's monkeys. Occasionally, they have been observed in larger groups, especially when several individuals were feeding on a large food source, for example at *Raphia* palms or on flying termites (HJR pers. obs.). In this study, we made no attempts to locate and observe individual birds. Instead, playback experiments were conducted independently of the presence or absence of birds. In other words, at the time when the experiments were carried out the presence of hornbills was a random factor.

Playback protocol

All playback experiments were carried out in the vicinity of a monkey group, whose behaviour was the main focus, as reported in other studies (*e.g.* Zuberbühler, 2003). The following six categories of vocalisations were used as playback stimuli (a) crowned eagle shrieks; (b) leopard growls; (c) Diana monkey eagle alarm calls; (d) Diana monkey leopard alarm calls; (e) Campbell's monkey eagle alarm calls; (f) Campbell's monkey leopard alarm calls. Leopard growls were purchased from the National Sound Archive, London. All other calls were recorded in the study area. All stimuli lasted for circa 15 s. Monkey alarm calls consisted of recordings of natural call series given by various adult males in response to crowned eagles or leopards. From the various master recordings we created the following 87 playback stimuli: eagle shrieks $N = 22$; leopard growls: $N = 27$; Diana monkey eagle alarm calls: $N = 10$; Diana monkey leopard alarm calls: $N = 11$; Campbell's eagle alarm calls: $N = 9$; Campbell's leopard alarm calls: $N = 8$. Figure 1 illustrates the various playback stimuli used in this study.

Throughout the eight-year study period, a total of 592 playback trials were carried out: 84 crowned eagle trials, 196 leopard trials, 60 Diana-eagle alarm call trials, 100 Diana-leopard alarm call trials, 77 Campbell's-eagle alarm call trials, and 75 Campbell's-leopard alarm call

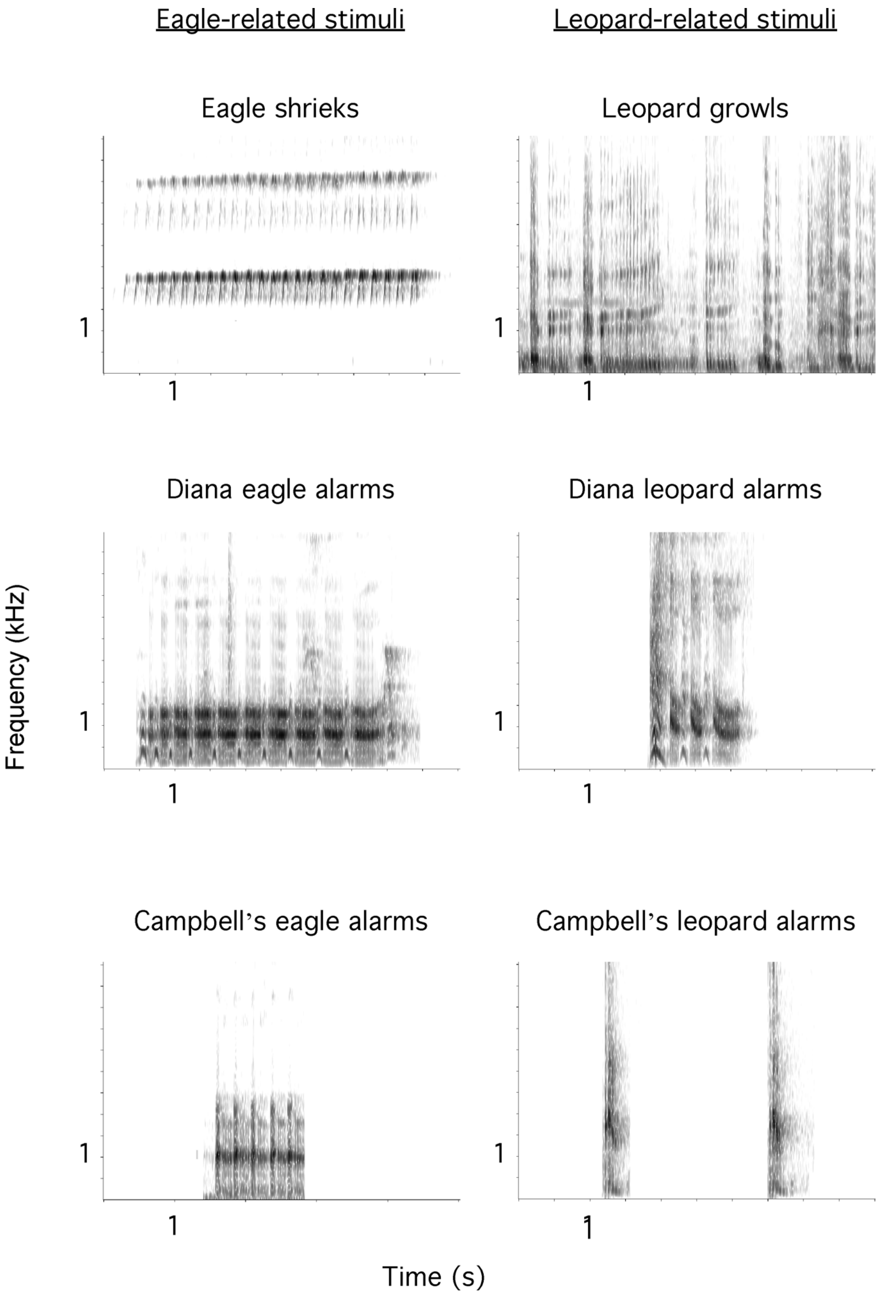

Fig. 1. Spectrographic representations of 5-s time slices of the six playback stimuli (vocalisations of a crowned eagle and leopard, male Diana and Campbell's monkey alarm calls to eagles and leopards): x-axis denotes time (s), y-axis denotes frequency (kHz); Spectrograms calculated using a Hanning window function; 512 points analysis resolution; 87.5% overlap; 4096 FFT size.

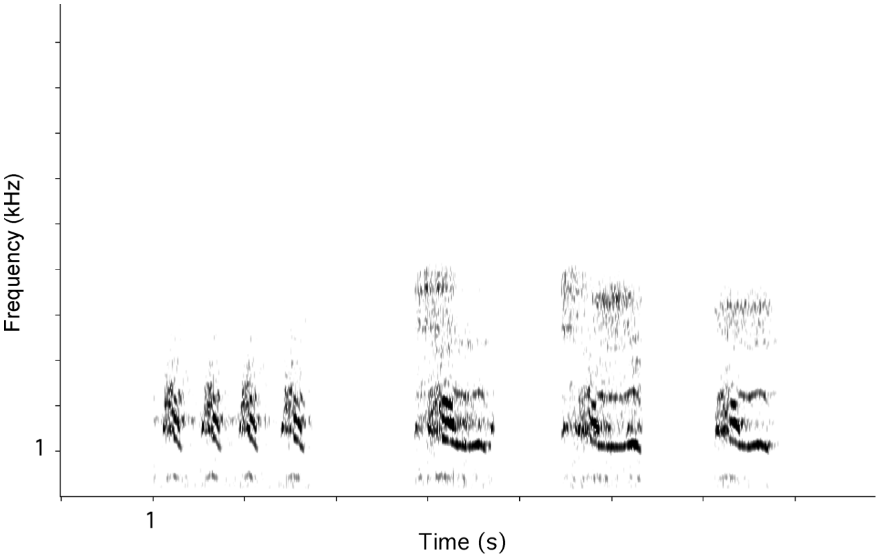

Fig. 2. Spectrographic representation of typical black-casqued hornbill calls given in response to eagle-related stimuli. X-axis denotes time (s), y-axis denotes frequency (kHz); Spectrograms calculated using Hanning window function; 512 points analysis resolution; 87.5% overlap; 4096 FFT size.

trials. Stimuli were played back at natural amplitudes varying from 88-110 dB. Each trial consisted of a 5 min pre-playback recording, followed by the playback stimulus, followed by a 5 min post-playback recording.

Acoustic observations

Most hornbill flocks consist of an adult male and female pair and one or two offspring with age- and sex-related differences in casque sizes (Kemp, 1995, HJR pers. obs.). The casque grows until the birds are adult and casques are sexually dimorphic. As the casque is likely to be involved in amplification and resonance of calls (Alexander *et al.*, 1994; Kemp, 1995), individuals of different ages and sexes within a small flock can be distinguished relatively easily. HJR screened all 592 10 min recordings for the presence of black-casqued hornbill vocalisations before and after the playback stimulus. Whenever calls of black-casqued hornbills could be identified, he noted the number of calls made by the first individual to call during the recording. We then compared the numbers of calls made before and after a playback stimulus across the different stimuli. Figure 2 illustrates typical black-casqued vocalisations.

Equipment

Playback stimuli were played back from a Sony WMD6C Professional Walkman through a Nagra DSM loudspeaker-amplifier. Peak amplitudes of each stimulus were standardised with a Radio Shack sound level meter 33-2050, C-weighting, at 1 m from the speaker. Recordings

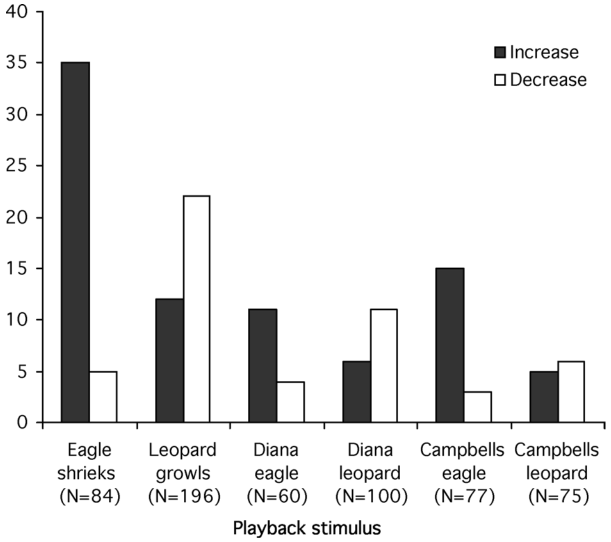

Fig. 3. Frequency of hornbill response types to different stimuli. Playbacks of eagle shrieks or monkey eagle alarm calls typically lead to an increase of calling behaviour, while playbacks of leopards or monkey leopard alarm calls had no effect. Black bars: increased call rates; grey bars: decreased calls call rates. Trials in which no bird responded are included in the overall N, but not plotted.

were made using a Sony TCM5000EV cassette recorder and a Sony WMD6C Professional Walkman with a Sennheiser ME66 directional microphone. Statistical analysis was carried out with SPSS 11.5.0 and Minitab 13. Recordings of calls were displayed as spectrograms with Avisoft-SASLab Pro 3.9, allowing us to count individual calls.

Results

Black-casqued hornbills increased call rates significantly more often in response to playbacks of eagle shrieks than leopard growls (Fisher's exact test: $N = 84, 196, p < 0.001$; Fig. 3). As predicted, they also increased call rates significantly more often to Diana-eagle than to Diana-leopard alarm calls (Fisher's exact test: $N = 60, 100, p = 0.018$; Fig. 3) as well as to Campbell's-eagle alarm calls than to Campbell's-leopard alarm calls (Fisher's exact test: $N = 77, 75, p = 0.029$; Fig. 3).

In a second analysis, we compared the actual call rates before and after a playback stimulus for those trials where we recorded at least one individual's calls. We found that all three eagle-related stimuli caused a significant

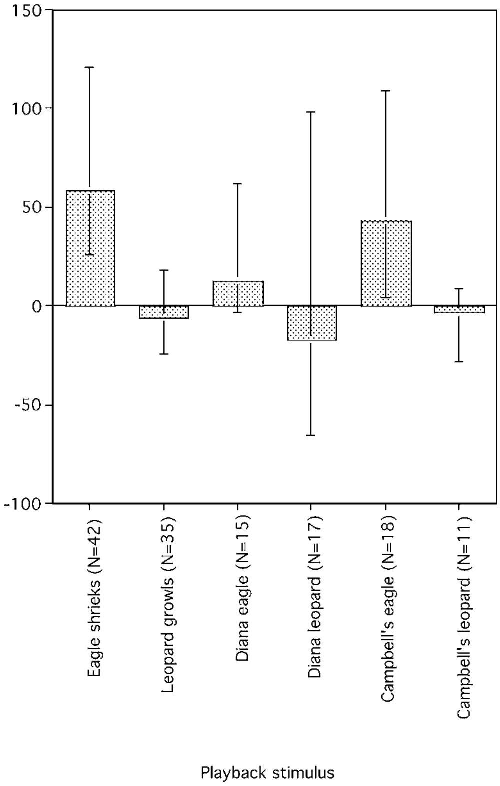

Fig. 4. Median and inter-quartile ranges of changes in call rates measured as difference between number of calls given 5 min before and after playback of each playback stimulus. Sample sizes refer to the numbers of trials in which changes in call rates occurred, *i.e.* those entering Wilcoxon statistical analyses.

increase in call rates, compared to the leopard-related stimuli where no significant changes were observed (Fig. 4). As the playback trials for this study were carried out independently of the presence or absence of hornbills, we controlled for the large numbers of trials on which no calls were recorded by analysing the change in numbers of calls produced between the 5 min before and after playback for each stimulus. We found that hornbills increased the numbers of calls they made to eagle shrieks (Wilcoxon signed rank test: $z = 799$, $N = 84$, $p < 0.001$) (Fig. 4a), to Diana-eagle calls (Wilcoxon signed rank test: $z = 97.5$, $N = 60$, $p = 0.036$) (Fig. 4b) and to Campbell's-eagle calls (Wilcoxon signed rank test: $z = 154$, $N = 77$, $p = 0.003$) (Fig. 4c). They did not increase the numbers of calls they made to leopard growls (Wilcoxon signed rank test, one tailed: $z = 259.5$, $N = 196$, $p = 0.521$) (Fig. 4d), to Diana-leopard calls (Wilcoxon signed rank test: $z = 83.0$, $N = 100$, $p = 0.931$) (Fig. 4e) or to Campbell's-leopard calls (Wilcoxon signed rank test: $z = 27.0$, $N = 75$, $p = 0.625$) (Fig. 4f).

Finally, we compared the hornbills' call rates when hearing the predator calls to their call rates when hearing the associated monkey alarm calls. Within the eagle-related stimuli we found that hornbills increased their call rates more often to eagle shrieks than to Diana-eagle alarm calls (Fisher's exact test: $N = 84, 60$, $p = 0.006$; Fig. 4). They also increased their call rates more often to eagle shrieks than to Campbell's-eagle alarm calls (Fisher's exact test: $N = 84, 77$, $p = 0.006$; Fig. 4). Bonferroni corrections did not affect the statistical significance of these results. In contrast, no significant changes were observed when we compared the hornbills' responses to leopard growls with Diana leopard (Fisher's exact test: $N = 196, 100$, $p = 1.0$; Fig. 4) or Campbell's leopard alarm calls (Fisher's exact test: $N = 196, 75$, $p = 1.0$; Fig. 4). Given the large numbers of playback trials when there was no change in response or no birds calling we excluded the no change category to demonstrate more clearly the variation in responses. There were no cases when birds called and made equal numbers of calls before and after playback.

Discussion

Hornbill responses to predator and primate calls

Our data suggest that in about half of all playback trials conducted one or several black-casqued hornbills were within the range of the playback stimulus. This is because, in about 48% of all trials involving eagle shrieks, the most powerful stimulus in eliciting vocal responses in hornbills, one or several birds vocalised in the 5 min period before and/or after the playback (Fig. 3). The overall response rate to leopards was much weaker (17%) and in most cases, no calls were given even though it is quite likely that birds were present. As we predicted, our data clearly showed that black-casqued hornbills distinguished between the calls of the two predators, as has been found in other hornbill species (Hauser & Wrangham, 1990; Rainey *et al.*, 2004).

Given that all playback trials were carried out in the presence of primate species, which often responded strongly to the stimuli, it is conceivable that the hornbills primarily responded to the behaviour of the primates rather than the playback stimuli themselves. Although the current design does not allow us to exclude this possibility a number of factors suggest that the birds indeed attended to the playback stimuli. First, the monkeys' locomotor responses (*e.g.* predator-specific flight responses) were unlikely to have affected the birds' vocal behaviour for two reasons. Forest monkeys do not normally show flight responses to leopards or eagles the way it has been described for savannah-living vervet monkeys (Seyfarth *et al.*, 1980). Instead, individuals often remain where they are, but instead increase their vigilance behaviour while giving predator-specific alarm calls. In addition, the visibility range in tropical rainforests is very low, often less than ten metres, suggesting that individuals cannot obtain crucial information through the visual mode. Second, if the birds simply attended to the primates' vocal responses to the playback stimuli, rather than to stimuli themselves, then their responses in eagle shriek and monkey eagle alarm call trials should be equivalent. However, our data revealed a much stronger response to eagle shrieks (Fig. 3), further suggesting that the birds were responding to the playback stimuli.

The effect of functionally referential primate alarm calls

Black-casqued hornbills were able to distinguish between the two different alarm calls produced by each monkey species. They responded to the Diana monkey eagle alarm call by increasing call rates, but not to the similar sounding Diana monkey leopard alarm calls (Fig. 3). An analogous pattern was found in response to the Campbell's monkey alarm calls (Fig. 3). Our results thus go beyond previous findings, in suggesting that black-casqued hornbills are able to acquire extensive knowledge of other species' communication systems. The ability of hornbills to distinguish between not only Diana monkey alarm calls, but also between Campbell's monkey alarm calls, is particularly remarkable. In comparison to the loud and conspicuous Diana monkeys, Campbell's monkeys are generally very cryptic in their overall behaviour, both visually and acoustically, and they produce alarm calls much less frequently (Wolters & Zuberbühler, 2003), suggesting that there may be many fewer learning opportunities for the birds.

Predator presence: the effect of spatial information

Our data showed that hornbills increased their call rates more often after playback of eagle shrieks than after either Diana-eagle calls or Campbell's-eagle calls. This finding was in line with the hypothesis that the birds may have attended to differences in spatial information concerning the predator's whereabouts. According to this scenario, hearing a predator provides more accurate information about the location of a predator than the corresponding primate alarm calls. Alarm calls may only signal that a particular predator is in the vicinity, but not its exact location. Perhaps, the hornbills behaved more cautiously when responding to monkey alarm calls, as these calls did not provide any information about the location of the predator (Rainey *et al.*, 2004). In yellowhammers individuals that had heard nearby conspecifics' alarm calls to a sparrow-hawk model were more alert and resumed foraging later than birds that saw the actual sparrow-hawk model (van der Veen, 2002; see Blumstein *et al.*, 2004 for additional examples).

Although the information precision hypothesis is an intriguing one, more rigorous testing will be required to confirm or refute it. At present, a simple arousal-based model could explain the data equally well: birds may simply have come to associate the presence of a crowned eagle with a highly aversive situation, relative to when hearing monkey eagle alarm calls, which often predict less dangerous situations. It is also conceivable that some birds, especially the younger ones, simply were not able to discriminate between the difference between the monkey alarm calls or were unaware that some of them predicted the presence of a crowned eagle.

The evolution of avian cognition

The ability to take advantage of environmental information regarding the type of predator present is relatively well described for non-human primates (*e.g.* Seyfarth *et al.*, 1980; Oda & Masataka, 1996; Zuberbühler, 2000). Here, we have provided further evidence that this ability is not restricted to mammals, by showing that hornbills can distinguish between different functionally referential alarm calls of non-human primates (see Rainey *et al.*, 2004). Interestingly, hornbills are exceptional amongst birds in that they exhibit a number of behaviours that are often considered indicators of more sophisticated cognitive capacities, including social interactions with members of other species. Rasa (1983) found that savannah hornbills *Tockus deckeni* and

T. flavirostris and dwarf mongooses *Helogale undulata* have a mutualistic relationship relating to predator detection and foraging. The birds are often first to respond to dangerous raptors and they are capable of distinguishing between different species of raptors (Rasa, 1983). Moreover, hornbills have relatively large brains and, unlike most other bird species, they exhibit social play (Diamond & Bond, 2003). Many large frugivorous hornbills are not territorial, as they require large numbers of ephemeral fruiting trees (Kemp, 1995, HJR pers. obs.). Defending a territory with a sufficient number of trees to maintain a family group throughout the year is likely to be uneconomical so that hornbills only appear to defend a small area around the nest site. Hornbills are long-lived and indulge in allopreening; many species breed cooperatively, including the *Ceratogymna* species (Kemp, 1995, HJR pers. obs.). Pairs of hornbills remain together for years and nest repeatedly with the same mate with young from previous years helping at the nest (Kalina, 1988; Kemp, 1995). These observations combine to suggest that there are similarities between the social systems of some hornbills and those of primates and that this may be conducive to the development of sophisticated cognitive abilities.

Future work will have to determine whether the hornbills' ability to recognise their predators by their vocalisations and to comprehend the alarm calls of the sympatric primates are unique amongst the numerous species of forest birds. The evidence suggests that hornbills do have sophisticated cognitive abilities (Rasa, 1983; Kemp, 1995; Diamond & Bond, 2003) but, as predation acts so strongly on future fitness (Lima & Dill, 1990), it might be expected that other bird species may be capable discriminating between the alarm calls of sympatric species.

References

Alexander, G.D., Houston, D.C. & Campbell, M. (1994). A possible acoustic function for the casque structure in hornbills (Aves: Bucerotidae). — J. Zool. (Lond.) 233, p. 57-67.

Blumstein, D.T., Verneyre, L. & Daniel, J.C. (2004). Reliability and the adaptive utility of discrimination among alarm callers. — Proc. Roy. Soc. B, 271, p. 1851-1857.

Bshary, R. & Noë, R. (1997). Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. — Behav. Ecol. Sociobiol. 41, p. 321-333.

Caro, T.M. (1995). Pursuit-deterrence revisited. — Trends Ecol. Evol. 10, p. 500-503.

Conover, M.R. (1987). Acquisition of predator information by active and passive mobbers in ring-billed gull colonies. — Behaviour 102, p. 41-57.

Curio, E. (1978). The adaptive significance of avian mobbing: I. Teleonomic hypotheses and predictions. — Z. Tierpsychol. 48, p. 175-183.

Diamond, J. & Bond, A.B. (2003). A comparative analysis of social play in birds. — Behaviour 140, p. 1091-1115.

Evans, C.S., Evans, L. & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. — Anim. Behav. 46, p. 23-38.

Hauser, M.D. & Wrangham, R.W. (1990). Recognition of predator and competitor calls in nonhuman primates and birds: a preliminary report. — Ethology 86, p. 116-130.

Hoppe-Dominik, B. (1984). Etude du spectres des proies de la panthère *Panthera pardus* dans le Parc National de Taï en Côte d'Ivoire. — Mammalia 48, p. 477-487.

Kalina, J. (1988). Ecology and behaviour of the black-and-white casqued hornbill (*Bycanistes subcylindricus subquadratus*) in Kibale Forest, Uganda. — PhD thesis, Michigan State University.

Keith, A.R. (1969). Crowned hawk-eagle raids hornbill nest. — J. E. Afr. Nat. Hist. Soc. 28, p. 64.

Kemp, A.C. (1995). The hornbills. — Oxford University Press, Oxford.

Kingdon, J. (1997). The Kingdon field guide to African mammals. — Academic Press, London.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. — Can. J. Zool. 68, p. 619-640.

Manser, M.B. (2001). The acoustic structure of suricates' alarm calls varies with the predator type and the level of response urgency. — Proc. Roy. Soc. Lond. B 268, p. 2315-2324.

Maynard Smith, J. (1965). The evolution of alarm calls. — Am. Nat. 99, p. 59-63.

Mitani, J.C., Sanders, W.J., Lwanga, J.S. & Windfelder, T.L. (2001). Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. — Behav. Ecol. Sociobiol. 49, p. 187-195.

Naguib, M., Mundry, R., Ostreiher, R., Hultsch, H., Schrader, L. & Todt, D. (1999). Cooperatively breeding Arabian babblers call differently when mobbing in different predator-induced situations. — Behav. Ecol. Sociobiol. 10, p. 636-640.

Oda, R. & Masataka, N. (1996). Interspecific responses of ring-tailed lemurs to playback of antipredator alarm calls given by Verreaux's sifakas. — Ethology 102, p. 441-453.

Rainey, H.J., Zuberbühler, K. & Slater, P.J.B. (2004). Hornbills can distinguish between primate alarm calls. — Proc. Roy. Soc. Lond. B 271, p. 755-759.

Rasa, O.A.E. (1983). Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. — Behav. Ecol. Sociobiol. 14, p. 181-190.

Ray, J.C. & Sunquist, M.E. (2001). Trophic relations in a community of African rainforest carnivores. — Oecologia 127, p. 395-408.

Seyfarth, R.M. & Cheney, D.L. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. — Anim. Behav. 40, p. 754-764.

— —, — — & Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. — Science 210, p. 801-803.

Shelley, E.L. & Blumstein, D.T. (in press). The evolution of vocal alarm communication in rodents. — Behav. Ecol.

Shultz, S.M. (2001). Notes on interactions between monkeys and African crowned eagles in Taï National Park, Ivory Coast. — Folia Primatol. 72, p. 248-250.

— — (2002). Population density, breeding chronology and diet of crowned eagles *Stephanoaetus coronatus* in Taï National Park, Ivory Coast. — Ibis 144, p. 135-138.

Slobodchikoff, C.N., Kiriazis, J., Fischer, C. & Creef, E. (1991). Semantic information distinguishing individuals predators in the alarm calls of Gunnison's prarie dogs. — Anim. Behav. 42, p. 713-719.

Tilson, R.L. & Norton, P.M. (1981). Alarm duetting and pursuit deterrence in an African antelope. — Am. Nat. 118, p. 455-462.

van der Veen, I.T. (2002). Seeing is believing: information about predators influences yellowhammers behaviour. — Behav. Ecol. Sociobiol. 51, p. 466-471.

Wolters, S. & Zuberbühler, K. (2003). Mixed species associations of Diana and Campbell's monkeys: the costs and benefits of a forest phenomenon. — Behaviour 140, p. 371-385.

Zuberbühler, K. (2000). Interspecies semantic communication in two forest primates. — Proc. Roy. Soc. Lond. B 267, p. 713-718.

— — (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. — Behav. Ecol. Sociobiol. 50, p. 414-422.

— — (2003). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language. — Adv. Study Behav. 33, p. 265-307.

— — & Jenny, D. (2002). Leopard predation and primate evolution. — J. Hum. Evol. 43, p. 873-886.

— —, — — & Bshary, R. (1999). The predator deterrence function of primate alarm calls. — Ethology 105, p. 477-490.

— —, Noë, R. & Seyfarth, R.M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. — Anim. Behav. 53, p. 589-604.