

Hornbills can distinguish between primate alarm calls

Hugo J. Rainey^{1*}, Klaus Zuberbühler² and Peter J. B. Slater¹

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 9ZU, UK*

Some mammals distinguish between and respond appropriately to the alarm calls of other mammal and bird species. However, the ability of birds to distinguish between mammal alarm calls has not been investigated. Diana monkeys (*Cercopithecus diana*) produce different alarm calls to two predators: crowned eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*). Yellow-casqued hornbills (*Ceratogymna elata*) are vulnerable to predation by crowned eagles but are not preyed on by leopards and might therefore be expected to respond to the Diana monkey eagle alarm call but not to the leopard alarm call. We compared responses of hornbills to playback of eagle shrieks, leopard growls, Diana monkey eagle alarm calls and Diana monkey leopard alarm calls and found that they distinguished appropriately between the two predator vocalizations as well as between the two Diana monkey alarm calls. We discuss possible mechanisms leading to these responses.

Keywords: interspecific communication; anti-predator behaviour; Ivory Coast; primates; associative learning; habituation

1. INTRODUCTION

Some mammals have been found to obtain information from the vocalizations of other species. Thus, various primates distinguish between and respond appropriately to the alarm calls of other primate species and of birds, as well as those of conspecifics (Seyfarth *et al.* 1980; Seyfarth & Cheney 1990; Zuberbühler 2000a). Some other mammal species have also been shown to respond appropriately to the calls of potential predators (Zuberbühler 2000b; Deecke *et al.* 2002) and of birds (Rasa 1983; Isack & Reyer 1989). Equivalent studies of birds have been more limited. While some birds have been found to respond appropriately to other species' alarm calls (Vieth *et al.* 1980; Nuechterlein 1981), there have been no studies of the abilities of wild birds to distinguish between the different alarm calls of another species.

Diana monkeys (*Cercopithecus diana*) produce different alarm calls to two of their main predators in West African forests: crowned eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*) (Zuberbühler *et al.* 1997). Yellow-casqued hornbills (*Ceratogymna elata*) are sympatric with both Diana monkeys and these two predators in many parts of their range. They are among the largest birds in the forest (mass of ca. 2 kg; Kemp 1995) and may be vulnerable to similar predators to Diana monkeys (mass of 2.2–7.5 kg; Kingdon 1997). Crowned eagles prey on hornbills, although they feed mostly on primates and small ungulates (Keith 1969; Mitani *et al.* 2001; Shultz 2002). However, leopards feed almost entirely on mammals (Hoppe-Dominik 1984; Ray & Sunquist 2001; Zuberbühler & Jenny 2002). While leopards do sometimes climb up to the canopy, where hornbills spend much of their time (Bshary & Noë 1997), and hornbills occasionally feed on the ground (H. J. Rainey, unpublished data), these are rare events.

As eagles prey on hornbills, we predicted that hornbills would respond to their calls. Similarly, as leopards are not thought to prey on hornbills, the birds should not respond to their calls. An appropriate response to a predator, including the production of alarm calls, may benefit both the individual calling and its relatives (Maynard Smith 1965; Charnov & Krebs 1975). Conversely, it would be of no benefit to hornbills to respond to leopard vocalizations if they are not subject to predation by leopards, and could even be costly if their response revealed their presence to another predator (Mougeot & Bretagnolle 2000) or reduced the time available for feeding (Caraco *et al.* 1980).

The most appropriate response of a prey species to the presence of a predator depends on the hunting behaviour of the predator. Eagles and leopards use surprise during an attack (Zuberbühler *et al.* 1999b; Shultz 2001). We predicted that hornbills would respond to the presence of a surprise predator by attempting to locate it and monitor its movements, thereby removing the element of surprise and reducing the chances of a successful attack (Curio 1978; Klump & Shalter 1984; Gautier-Hion & Tutin 1988). Hornbills in Ivory Coast mob crowned eagles by calling and approaching the predator (S. Shultz, unpublished data). We also predicted that hornbills would produce alarm calls to alert others to the presence of the predator (Frankenberg 1981) or to signal that it has been detected (the 'perception advertisement' hypothesis; Curio 1978). Zuberbühler *et al.* (1999b) showed that primate alarm calls deterred leopards from hunting and caused them to leave the area. There is also some evidence that crowned eagles are deterred from hunting on hearing Diana monkey alarm calls (Shultz 2001).

As hornbills are often found close to Diana monkeys, sometimes feeding in the same trees, they are likely to hear each other's calls frequently. They may, therefore, associate the two different Diana monkey alarm calls with the presence of the corresponding predators and thus come to respond appropriately. As eagles (but not leopards) are

* Author for correspondence (hjr3@st-andrews.ac.uk).

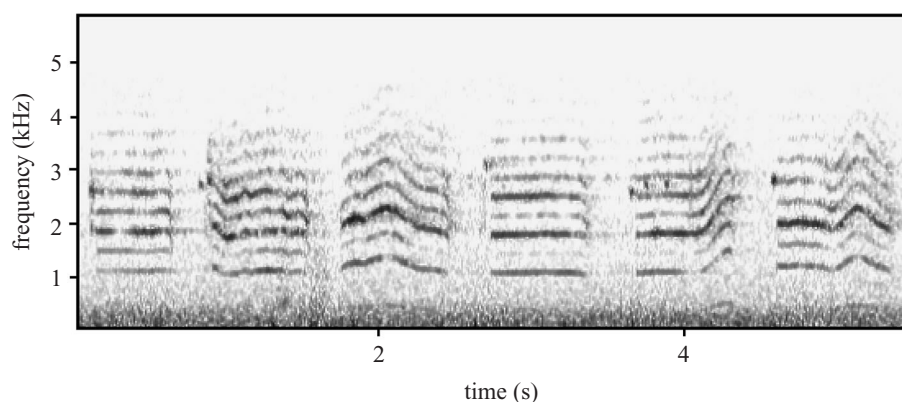


Figure 1. Spectrogram of typical yellow-casqued hornbill calls.

predators of hornbills, we predicted that hornbills would respond to the Diana monkey eagle alarm call but not to the Diana monkey leopard alarm call.

2. MATERIAL AND METHODS

(a) *Study site*

H.J.R. carried out the fieldwork in Taï and Mont Péko National Parks, Ivory Coast, between October 2001 and May 2002 inclusive. In Taï, the work was based in two areas: *ca.* 70 km² around the Centre de Recherche en Ecologie (5°50' N, 7°21' W) and *ca.* 25 km² near the Ecotel at Guiroutou (5°24' N, 7°15' W). In Mont Péko, the area covered was *ca.* 15 km² in the north of the park near Goenié (7°06' N, 7°16' W).

(b) *Selecting hornbill flocks*

The observer located yellow-casqued hornbills during systematic searching by listening for their vocalizations and noisy wing-beats and occasionally by direct observations (both forests are dense and visibility is limited). To maximize the independence of each playback trial, playbacks were separated spatially by at least 500 m or, if within 500 m, temporally by at least four months to reduce the chance of hornbills becoming habituated to a particular stimulus type. This is a realistic separation as natural predators such as the crowned eagle can attack a single monkey group several times in a day (Zuberbühler *et al.* 1997). We worked at three different sites, and hornbills range and migrate widely both within and between seasons (Poonswad & Tsuji 1994; Holbrook *et al.* 2002), so, although the hornbills could not be recognized individually, it is highly unlikely that any two trials involved the same individual.

(c) *Playback protocol*

Pilot work in Mont Péko found that hornbills have low calling rates, reduced activity and low response rates before 07.00 and after 13.00, so all the experiments took place between these times. When a flock was located, the observer approached to within 50 m so that the vocalization played back was close enough to be of immediate importance to the birds. The speaker was placed at a height of *ca.* 2 m above the ground to reduce attenuation of the sound. Diana monkeys and both species of predator can be found at ground level (H. J. Rainey and K. Zuberbühler, unpublished data). The experiment was begun only if there was no predator present and if alarm calls had not been produced by hornbills, primates or other animals in the area within 10 min of the start of recording and if the birds had

not responded to the observer's approach. If hornbills noticed the observer they often flew off.

Once a hornbill flock had been approached, an adult individual, usually a male, was located and notes were taken of its behaviour. Adult females were selected only if they could be distinguished clearly from immature birds using both vocal behaviour and plumage (Kemp 1995; H. J. Rainey, unpublished data). We focused on adult individuals, as they were more likely to have experienced interactions between Diana monkeys and predators. Yellow-casqued hornbill flocks consist of small family groups containing at least one adult male and one adult female with one or two immature birds. Occasionally individual birds or pairs were located, and on one occasion a flock of more than 30 birds was encountered feeding on flying ants or termites. In all but six playback tests an adult male was present in the flock and targeted for observations.

The following four categories of vocalization were used as playback stimuli:

- (i) crowned eagle shrieks—15 s of continuous recording;
- (ii) leopard growls—15 s of continuous recording;
- (iii) Diana monkey alarm calls in response to a crowned eagle—15 s of recordings containing three calls;
- (iv) Diana monkey alarm calls in response to a leopard—15 s of recordings containing four calls (this call consists of fewer syllables than the Diana monkey eagle alarm call; Zuberbühler *et al.* 1997).

Crowned eagle shrieks were obtained from commercial recordings (Chappuis 2001) and leopard growls from the National Sound Archive, London. Diana monkey alarm calls of both types had been recorded by K.Z. in Taï (see Zuberbühler *et al.* (1997) for spectrograms of all four stimuli). Eagle shrieks and leopard growls from different individuals were natural sequences each lasting 15 s. We used alarm call sequences from six different male Diana monkeys; three of these were eagle alarm calls and three were leopard alarm calls. Three or four calls (see above) from an individual calling sequence were selected for each playback exemplar. We used three different exemplars of each category to avoid pseudoreplication (Kroodsma 1989). We carried out a total of 34 playback trials: four in Mont Péko and 30 in Taï. One recording was corrupted and could not be used for analysis although observational data were obtained from this trial. After 5 min of tape recording and behavioural observations, one of the stimuli was played back for a total of 15 s, followed by a further 5 min of recording and observations.

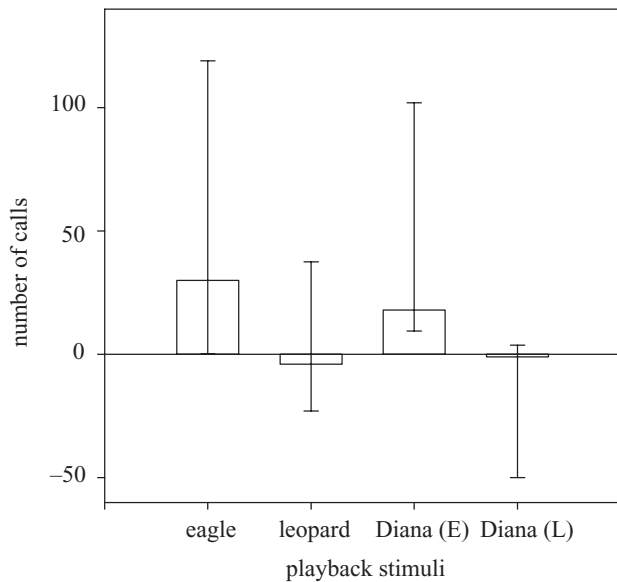


Figure 2. Medians and interquartile ranges of differences between the numbers of calls made before and after playback of different stimulus types. Hornbills increased the differences between the numbers of calls more after eagle playback than after leopard playback, $p < 0.001$; and hornbills increased the differences between the numbers of calls more after Diana monkey eagle playback than after Diana monkey leopard playback, $p < 0.001$.

(d) Observational notes

We noted the times at which the focal individual called, and this allowed us to separate its calls from those of other individuals. Yellow-casqued hornbill calls often have resonant harmonics and are nasal in tone (see figure 1). As hornbills have noisy wingbeats it was possible to follow their movements even when dense vegetation limited visual observation. We made notes on the focal bird's movements with respect to the playback site and on the behaviour before and after playback. Classification of movement as being towards or away from the playback site was based on the first movement between branches or trees (rather than along a branch). The rationale for this was that, as greater effort is generally needed to move between branches than along a branch, such movement would be more likely to relate to the stimulus. The direction of movement was classed as being in the 180° segment towards or away from the playback site. In fact, almost all movements were at a narrow angle to the playback site.

(e) Equipment

The stimuli were played back from a Goodmans GCD506R CD player through a Nagra DSM loudspeaker amplifier. Peak amplitudes of each stimulus were standardized at *ca.* 95 dB with a Tenma Sound Level Meter 72-6604, A-weighting, at 1 m from the speaker. Audible responses were recorded using a Sony WMD6C Professional Walkman with a Sennheiser ME66 microphone. MINITAB 12 was used for statistical analysis. Recordings of calls were displayed as spectrograms with Avisoft-SASLAB PRO v. 3.9 on which individual calls could be counted.

3. RESULTS

(a) Vocal behaviour

The differences in the total numbers of calls in the 5 min before and after playback indicated that hornbills

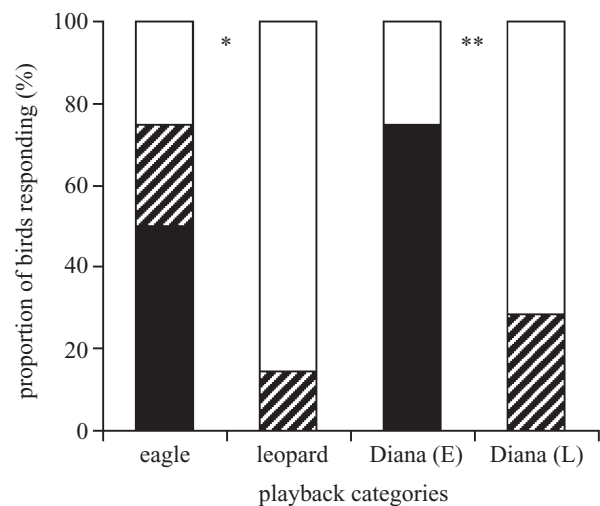


Figure 3. Proportions of hornbills approaching, departing from and not moving in relation to the playback site in response to different playback stimuli. Black bars, approach; hatched bars, depart; open bars, no movement. *Hornbills approached eagle playback more often than leopard playback, $p = 0.03$. **Hornbills approached Diana monkey eagle playback more often than Diana monkey leopard playback, $p = 0.006$.

called significantly more after some playback types than others (Kruskal–Wallis test: $H_3 = 8.6$, $p = 0.035$; figure 2). *Post-hoc* non-parametric multiple comparison (Zar 1999) showed that hornbills called significantly more after playback of eagle shrieks than after playback of leopard growls ($Q_4 = 8.22$, $n = 11,7$, $p < 0.001$). Similarly, hornbills called significantly more after playback of Diana monkey eagle alarm calls than after playback of Diana monkey leopard alarm calls ($Q_4 = 8.39$, $n = 8,7$, $p < 0.001$).

(b) Locomotor behaviour

As figure 3 shows, hornbills approached the playback site significantly more often in response to playback of eagle shrieks than playback of leopard growls (Fisher's exact test: $n = 12,7$, $p = 0.03$). Hornbills also approached the playback site more often in response to playback of the Diana monkey eagle alarm call than the Diana monkey leopard alarm call (Fisher's exact test: $n = 8,7$, $p = 0.006$). No differences between approaches to eagle shrieks and Diana monkey eagle alarm calls (Fisher's exact test: $n = 12,8$, $p = 0.26$) nor between approaches to leopard growls and Diana monkey leopard alarm calls were found (Fisher's exact test: $n = 7,7$, $p = 1$; figure 3).

4. DISCUSSION

Our results indicate that yellow-casqued hornbills distinguish between predator vocalizations and between the corresponding alarm calls of the sympatric Diana monkey. Both vocal and locomotor responses of hornbills to playback of eagle shrieks and Diana monkey eagle alarm calls were significantly different from the responses to playback of leopard growls and Diana monkey leopard alarm calls. This is the first time, to our knowledge, that a bird has been shown to distinguish between the alarm calls of any other species and the first time that they have been found to distinguish between mammal calls of any type. The

result is particularly intriguing as the two Diana monkey alarm calls are acoustically very similar (see Zuberbühler *et al.* 1997).

Our sample sizes were small, and the statistical analyses may have had low power to detect significant results (Thomas & Juanes 1996). However, we had matched controls (eagle to leopard and Diana monkey eagle call to Diana monkey leopard call), which also had small sample sizes, yet the effects were still significant. This indicates that, despite this low power, the responses varied between the different playback categories. We could not test for a difference between the responses of male and female hornbills to the different stimuli as sample sizes were too small. However, both sexes exhibited all types of response so it is probable that they respond similarly. The hornbills also showed similar variation in responses to the four trials in Mont Péko and this indicates that, despite the small sample size, the responses here were representative.

The 'perception advertisement' hypothesis (Curio 1978) suggests that animals may produce alarm calls when they detect a predator because this indicates to the predator that it has been detected and that it has lost the element of surprise. An attack would therefore probably fail, and the predator would best abandon the attack. This may explain the tendency of hornbills, and of primates (Gautier-Hion & Tutin 1988; Zuberbühler *et al.* 1997), to approach the predator as it demonstrates more clearly to the predator that it has been located. There were indications that hornbills tended to approach the playback site more often after playback of Diana monkey eagle alarm calls than after playback of eagle shrieks (figure 3). This difference was not significant but could indicate that, because alarm calls unlike predator calls do not indicate the precise location of the predator (Van der Veen 2002), the hornbills may best locate the predator by approaching the alarm call. This may help the bird to decide in which direction to flee or whether or not to mob the predator. It is therefore possible that hornbills are advertising perception to the predator (Curio 1978) and that the alarm signals may not be directed at kin (Maynard Smith 1965).

How do hornbills acquire the ability to distinguish between the four different types of vocalizations? Animal learning theory offers a number of mechanisms that may be responsible for the birds' knowledge. First, many mature birds will have experienced attacks by crowned eagles, either directly or indirectly by observing other nearby individuals being attacked. As both eagle shrieks and Diana monkey eagle alarm calls reliably predict the presence of a crowned eagle in the immediate vicinity, both stimuli will quickly become associated with eagle presence through associative learning. Second, young birds may learn to respond to the eagle shrieks and Diana monkey eagle alarm calls by observing other, more experienced, flock members reacting to these calls, even in the absence of direct contact with the predator. Observing other individuals engaging in anti-predator behaviour is a powerful stimulus and a reliable source for rapid learning (Curio *et al.* 1978; Vieth *et al.* 1980; Frankenberg 1981). As leopards do not attack hornbills, no such learning will take place, and consequently both leopard growls and Diana monkey leopard alarm calls will not come to elicit responses in hornbills. An alternative hypothesis states that hornbills will call spontaneously in response to any

loud stimulus, but through individual experience they selectively habituate to those stimuli that do not predict the presence of a species that preys on them (i.e. leopard growls and Diana monkey leopard alarm calls; see Deecke *et al.* 2002).

Our findings suggest that eagle shrieks and Diana monkey eagle alarm calls are functionally equivalent for hornbills (Schusterman & Gisiner 1997), in the sense that they both predict the presence of a crowned eagle. But are they linked to a mental representation of the predator, as has been claimed for non-human primates (Zuberbühler *et al.* 1999a)? We can say little yet about the mental processes that underlie the birds' responses. What is remarkable is that, although the acoustic differences between the two types of Diana monkey alarm calls are very subtle, the hornbills respond differently to them, demonstrating how active these animals are in their pursuit of important information, to the extent of eavesdropping on signals that are not intended for them.

The authors thank Dr J. Tondoh for providing permits. Cdt. A. Dje Bi Ta, Lt. O. Justin, Adj. G. Manh and A. Kragbé in Mont Péko and the staff at the Centre de Recherche en Ecologie were very helpful. G. Rondeau, A. Dro, C. Sugden and H. Curtis very kindly gave logistical support. H.J.R. received financial support from St Andrews University. C. Short and L. Alonso of Conservation International and F. Lauginie of Afrique Nature International provided funding opportunities. M. Ritchie, J. Graves and S. Ward gave statistical advice. S. Shultz gave details of eagle behaviour. The authors thank three anonymous referees for their helpful comments.

REFERENCES

- Bshary, R. & Noë, R. 1997 Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behav. Ecol. Sociobiol.* **41**, 321–333.
- Caraco, T., Martindale, S. & Pulliam, H. R. 1980 Avian flocking in the presence of a predator. *Nature* **285**, 400–401.
- Chappuis, C. 2001 *Oiseaux d'Afrique—African bird sounds*, Vol. 2. Paris: SEOF, Musée Nationale d'Histoire Naturelle.
- Charnov, E. L. & Krebs, J. R. 1975 Evolution of alarm calls: altruism or manipulation? *Am. Nat.* **109**, 107–112.
- Curio, E. 1978 The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Z. Tierpsychol.* **48**, 175–183.
- Curio, E., Ernst, U. & Vieth, W. 1978 The adaptive significance of avian mobbing. II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. *Z. Tierpsychol.* **48**, 184–202.
- Deecke, V. B., Slater, P. J. B. & Ford, J. K. B. 2002 Selective habituation shapes acoustic predator recognition in harbour seals. *Nature* **420**, 171–173. (DOI 10.1038/nature01030.)
- Frankenberg, E. 1981 The adaptive significance of avian mobbing. IV. 'Alerting others' and 'perception advertisement' in blackbirds facing an owl. *Z. Tierpsychol.* **55**, 97–118.
- Gautier-Hion, A. & Tutin, C. E. G. 1988 Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatol.* **51**, 149–151.
- Holbrook, K. M., Smith, T. B. & Hardesty, B. D. 2002 Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* **25**, 745–749.
- Hoppe-Dominik, B. 1984 Etude du spectre des proies de la panthère *Panthera pardus* dans le Parc National de Tai en Côte d'Ivoire. *Mammalia* **48**, 477–487.

- Isack, H. A. & Reyer, H.-U. 1989 Honeyguides and honey gatherers: interspecific communication in a symbiotic relationship. *Science* **243**, 1343–1346.
- Keith, A. R. 1969 Crowned hawk-eagle raids hornbill nest. *J. E. Afr. Nat. Hist. Soc.* **28**, 64.
- Kemp, A. C. 1995 *The hornbills*. Oxford University Press.
- Kingdon, J. 1997 *The Kingdon field guide to African mammals*. London: Academic.
- Klump, G. M. & Shalter, M. D. 1984 Acoustic behaviour of birds and mammals in the predator context. *Z. Tierpsychol.* **66**, 189–226.
- Kroodtsma, D. E. 1989 Suggested experimental designs for song playbacks. *Anim. Behav.* **37**, 600–609.
- Maynard Smith, J. 1965 The evolution of alarm calls. *Am. Nat.* **99**, 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**, 187–195.
- Mougeot, F. & Bretagnolle, V. 2000 Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Anim. Behav.* **60**, 647–656.
- Nuechterlein, G. L. 1981 'Information parasitism' in mixed colonies of western grebes and Forster's terns. *Anim. Behav.* **29**, 985–989.
- Poonswad, P. & Tsuji, A. 1994 Ranges of males of the great hornbill *Buceros bicornis*, brown hornbill *Ptilolaemus tickelli* and wreathed hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis* **136**, 79–86.
- Rasa, O. A. E. 1983 Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. *Behav. Ecol. Sociobiol.* **14**, 181–190.
- Ray, J. C. & Sunquist, M. E. 2001 Trophic relations in a community of African rainforest carnivores. *Oecologia* **127**, 395–408.
- Schusterman, R. J. & Gisiner, R. C. 1997 Pinnipeds, porpoises and parsimony: animal language research viewed from a bottom-up perspective. In *Anthropomorphism, anecdotes, and animals* (ed. R. W. Mitchell, N. S. Thompson & H. L. Miles), pp. 370–382. Lincoln, NB: University of Nebraska.
- Seyfarth, R. M. & Cheney, D. L. 1990 The assessment by vervet monkeys of their own and another species' alarm calls. *Anim. Behav.* **40**, 754–764.
- Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980 Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* **210**, 801–803.
- Shultz, S. M. 2001 Notes on interactions between monkeys and African crowned eagles in Tai National Park, Ivory Coast. *Folia Primatol.* **72**, 248–250.
- Shultz, S. M. 2002 Population density, breeding chronology and diet of crowned eagles *Stephanoaetus coronatus* in Tai National Park, Ivory Coast. *Ibis* **144**, 135–138.
- Thomas, L. & Juanes, F. 1996 The importance of statistical power analysis: an example from *Animal Behaviour*. *Anim. Behav.* **52**, 856–859.
- Van der Veen, I. T. 2002 Seeing is believing: information about predators influences yellowhammers behaviour. *Behav. Ecol. Sociobiol.* **51**, 466–471. (DOI 10.1007/s00265-002-0464-4.)
- Vieth, W., Curio, E. & Ernst, U. 1980 The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: cross-species tutoring and properties of learning. *Anim. Behav.* **28**, 1217–1229.
- Zar, J. H. 1999 *Biostatistical analysis*, 4th edn. London: Prentice-Hall.
- Zuberbühler, K. 2000a Interspecies semantic communication in two forest primates. *Proc. R. Soc. Lond. B* **267**, 713–718. (DOI 10.1098/rspb.2000.1061.)
- Zuberbühler, K. 2000b Causal knowledge of predators' behaviour in wild Diana monkeys. *Anim. Behav.* **59**, 209–220.
- Zuberbühler, K. & Jenny, D. 2002 Leopard predation and primate evolution. *J. Hum. Evol.* **43**, 873–886.
- Zuberbühler, K., Noë, R. & Seyfarth, R. M. 1997 Diana monkey long-distance calls: messages for conspecifics and predators. *Anim. Behav.* **53**, 589–604.
- Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. 1999a Conceptual semantics in a non-human primate. *J. Comp. Psychol.* **113**, 33–42.
- Zuberbühler, K., Jenny, D. & Bshary, R. 1999b The predator deterrence function of primate calls. *Ethology* **105**, 477–490.