Baboon responses to graded bark variants

JULIA FISCHER*, MARKUS METZ†, DOROTHY L. CHENEY* & ROBERT M. SEYFARTH*

*Departments of Psychology and Biology, University of Pennsylvania
†Institut für Verhaltensbiologie, Freie Universität Berlin

We studied chacma baboons', *Papio cynocephalus ursinus*, responses to conspecific 'barks' in a free-ranging population in the Okavango Delta of Botswana. These barks grade from tonal, harmonically rich calls to calls having a noisier, harsher structure. Tonal or clear barks are typically given when the signaller is at risk of losing contact with the group or when a mother and infant have become separated ('contact barks'). The harsher variants are given in response to predators ('alarm barks'). In both contexts, however, we also observed acoustically intermediate forms. Using the habituation–recovery method we tested whether baboons discriminated between (1) clear contact barks versus harsh alarm barks, and (2) clear contact barks versus intermediate alarm barks. Calls were selected according to the results of a discriminant function analysis conducted on a suite of acoustic parameters. In these experiments, animals showed a significant recovery of response only after playback of the harsh alarm call. We performed another set of experiments using single exemplars of clear and intermediate contact barks, or intermediate and harsh alarm barks. Animals responded only to the playback of a harsh alarm bark. Apparently, only this harsh variant was placed in a category that warranted a response. We hypothesize that baboons' responses were to a large degree influenced by their assessment of context.

© 2001 The Association for the Study of Animal Behaviour

Peter Marler (1975) hypothesized that a crucial stage in the evolution of human language occurred when individuals began to perceive a graded continuum of sounds as a series of discrete categories. Although there is good evidence that nonhuman primates perceive some acoustically graded calls as conveying qualitatively different information (Pola & Snowdon 1975; Marler 1976; Seyfarth & Cheney 1984; Gouzoules & Gouzoules 1989; Hauser 1991; Hauser & Marler 1993; Mitani 1996; Rendall et al. 1999), to our knowledge only two studies have investigated how individuals respond to calls that fall at the acoustic boundary of two categories. In the first such study, Snowdon & Pola (1978) examined pygmy marmosets', *Cebuella pygmaea*, responses to synthetic modifications of trills. Two types of trills were given, the closed-mouth and the open-mouth trill, varying mainly in trill duration. Closed-mouth trills are used in quiet,

contact-seeking situations and often elicit antiphonal calling in other animals, whereas open-mouth trills are mainly associated with fearful or aggressive behaviour and do not elicit antiphonal calling. A systematic variation in trill duration revealed a distinct drop in the rate of antiphonal calling at the category boundary. More recently, Fischer (1998) used the habituation–recovery method to investigate the responses given by Barbary macaques, *Macaca sylvanus*, to two categories of shrill alarm barks. Subjects discriminated reliably between calls of the two categories irrespective of the acoustic difference between pairs, but failed to discriminate members of the same category. Barbary macaques thus responded in a categorical fashion to variation in an acoustic continuum (Fischer 1998).

In the present study, we aimed to replicate the earlier findings on Barbary macaques in free-ranging chacma baboons, *Papio cynocephalus ursinus*. Specifically, we examined the extent to which listeners discriminated among different variants of females' loud barks. These barks constitute a graded continuum, ranging from tonal, harmonically rich calls to calls having a noisier, harsher structure. A detailed acoustical analysis (Fischer et al. 2001) has revealed that the more tonal 'clear barks' (Hall & DeVore 1965; Byrne 1981) are typically given when the signaller is at risk of losing contact with the group or when a mother and infant have become separated.

Correspondence and present addresses: J. Fischer, Max-Planck Institute for Evolutionary Anthropology, Inselstraße 22, 04103 Leipzig, Germany (email: fischer@eva.mpg.de). M. Metz is now at the Institut für Zoologie, Technische Universität München, Lichtenbergstraße 4, 85748 Garching, Germany. D. L. Cheney is at the Department of Biology, University of Pennsylvania, Leidy Building, 415 South University Avenue, Philadelphia, PA 19104, U.S.A. R. M. Seyfarth is at the Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, PA 19104, U.S.A.

Accordingly, these have also been termed 'contact barks' (Cheney et al. 1996; Rendall et al. 2000). The harsher variants, 'sharp' or 'shrill barks' (Hall & DeVore 1965), are given in response to predators. We therefore term these barks 'alarm barks'. Acoustic analysis, however, has also revealed that intermediate forms between the two subtypes sometimes occur in both situations (Fischer et al. 2001).

Previous observations and experiments have indicated that baboons respond strongly to alarm barks of both related and unrelated individuals, either by looking towards the signaller or by running towards trees (D. L. Cheney, R. M. Seyfarth, unpublished data). In contrast, they respond weakly if at all to unrelated individuals' contact barks, and somewhat more strongly to contact barks of related individuals (Cheney et al. 1996; Rendall et al. 2000). These observations suggest that baboons generally respond quite differently to the two call categories, presumably because a failure to respond to alarm barks incurs a greater cost than a failure to respond to a contact bark. In the first set of experiments, we used the habituation–recovery method to test whether subjects discriminated between typical variants of contact barks and either typical or intermediate variants of alarm barks. We predicted that subjects would respond strongly to the alarm barks, regardless of whether they were acoustically more or less distinct from contact barks. In another set of experiments, we examined baboons' responses to the presentation of single exemplars of typical and intermediate alarm and contact barks. We predicted that they would respond strongly to playbacks of harsh and intermediate alarm barks and perhaps also to intermediate contact barks, but only weakly to typical contact barks.

METHODS

Study Site and Subjects

The study site lies in the Moremi Wildlife Reserve, Botswana, southern Africa, in the Okavango Delta, a huge inland delta fed by the Okavango River. Yearly rainfall in the mountainous regions of Angola causes the Okavango and its tributaries to rise and flood the grasslands. Only slightly elevated patches of woodland, or 'islands', which range in size from less than one to over hundreds of hectares, remain uncovered. During the flood, the baboons ford the floodplains to travel from one island to the next (Hamilton et al. 1976; Ross 1987).

The average size of a baboon troop's home range in the area is 450 ha (range 210–650 ha) (Hamilton et al. 1976). The study group, Group C, has been observed more or less continuously for more than 20 years. The matrilineal relatedness of all natal animals born since 1978 is known. A number of comprehensive studies on the social behaviour have been published, as well as on the vocal communication of this population (see references in Cheney & Seyfarth 1999). During the period of this study, group size ranged from 79 to 84 subjects, including 26 females, 13 immigrant adult males, and 15 subadult and adult natal males, aged 6 years or more.
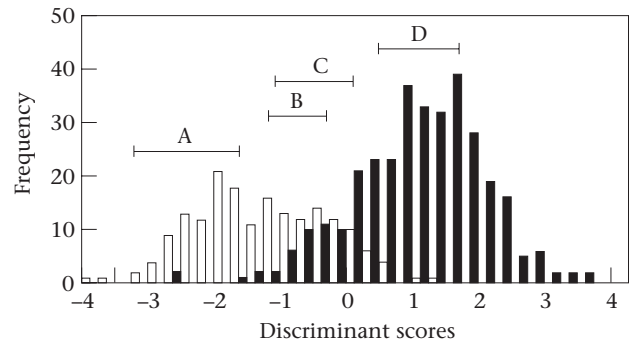

Figure 1. Distribution of discriminant scores as derived from the acoustic analysis and selection of calls for playback. □: Alarm barks; ■: contact barks. Calls represented at the tail ends of the distribution differ most. Horizontal lines depict the range of the discriminant scores for the four acoustic categories established for playback. A: typical alarm barks; B: intermediate alarm barks; C: intermediate contact barks; D: typical contact barks.

Call selection

We recorded 'contact barks' when the signaller was separated from the group, either alone or with a small party of other animals, or when a female had apparently lost contact with her infant. We recorded 'alarm barks' when the signaller had either spotted lions (*Panthera leo*) or crocodiles (*Crocodilus niloticus*). We selected the calls for playback according to the results of an acoustic analysis presented in detail elsewhere (Fischer et al. 2001). Briefly, calls were digitized and submitted to a fast Fourier transform. We applied a custom software programme developed by Kurt Hammerschmidt (LMA 8.7) that automatically extracts a large set of acoustic parameters. We then used a discriminant function analysis to examine the differences between the two categories, 'alarm' and 'contact' barks. In dealing with two groups, the discriminant function analysis assigns one discriminant score to each case in the analysis. We used the discriminant score in which the multivariate variability of calls is collapsed into a single number as a measure of acoustic similarity.

According to the outcome of this analysis, the two call categories represent a nondiscrete acoustic continuum. Within this continuum, we used the values of the discriminant score to establish four sets of calls that differed in their acoustic similarity: 'harsh alarm barks', 'intermediate alarm barks', 'intermediate contact barks' and 'clear contact barks'. 'Clear contact barks' and 'harsh alarm barks' show the largest acoustic difference, whereas 'intermediate' alarm and contact barks fall between the two extremes. We defined harsh alarm barks and clear contact barks as 'typical' exemplars of their respective context categories. In summary, we established call sets according to the context in which they were given and their acoustic characteristics. Figure 1 shows the frequency distribution of discriminant coefficients and the range according to which calls were selected for playback.
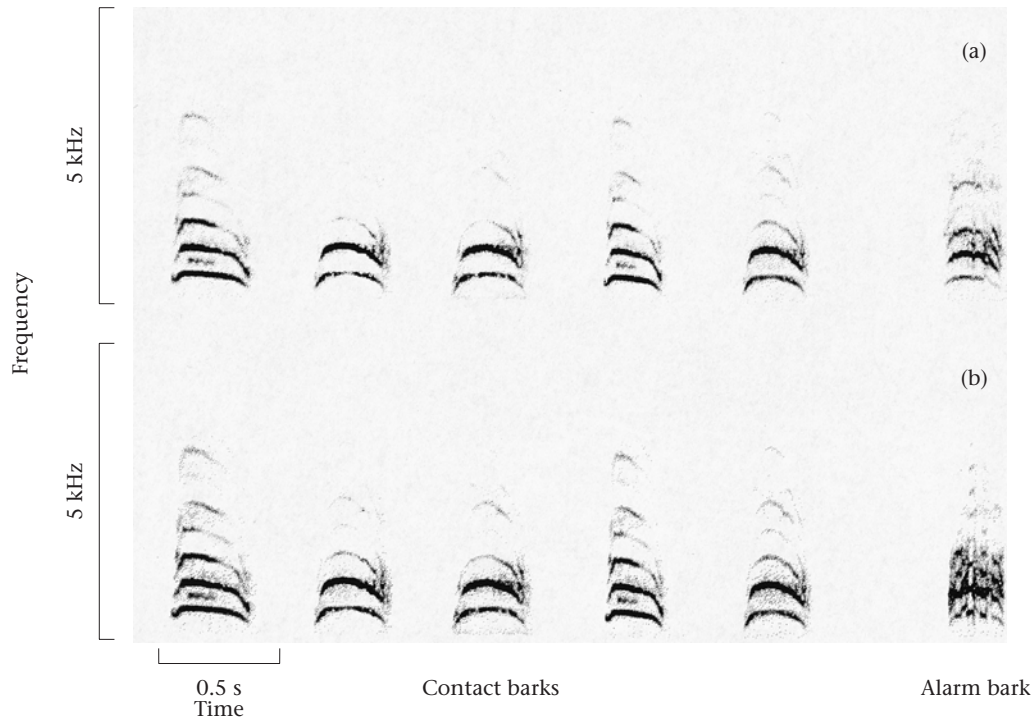
Figure 2. Examples of calls used for habituation and in the test trial. Five typical contact barks recorded from one female were used for habituation, then either (a) an intermediate variant of an alarm bark or (b) a typical variant of an alarm bark was played.

Experimental Protocol

Habituation experiments

To test whether baboons discriminate among different variants of contact and alarm barks, we used the habituation–recovery method. With this technique, stimuli of one category are repeatedly presented until the subject habituates. Then, a stimulus from a putative different category is presented. A revival of response (recovery) suggests that the test stimulus provides novel information to the subject. One can therefore assume that the test stimulus is placed in a different category from that of the stimuli used for habituation (Hauser 1996; Wyttenbach & Hoy 2000). Cheney & Seyfarth (1988) were the first to use this technique in free-ranging nonhuman primates, testing the hypothesis that vervet monkey, *Cercopithecus aethiops*, calls are 'functionally referential' (Cheney & Seyfarth 1990; Marler et al. 1992). Subsequently, the method has been used successfully in a variety of other nonhuman primate studies (Rendall et al. 1996; Fischer 1998; Hauser 1998).

We conducted two sets of experiments to test whether subjects discriminated between (1) clear variants of contact barks and harsh variants of alarm barks ('distinct' design), and (2) clear variants of contact barks and intermediate variants of alarm barks ('intermediate' design). In other words, even in the 'intermediate' design, calls used for habituation and in the test were still markedly different. We did not test the reverse design (i.e. habituate with alarm barks and then play a contact bark in the test), because we suspected that subjects would run away after multiple playbacks of alarm calls. Equally important,

contact barks generally elicit much weaker responses than alarm barks, so even if the subjects perceived a meaningful difference, it would have been difficult to detect this in their behaviour.

For the experiments, we constructed series of five typical contact barks followed by either a distinct or an intermediate alarm bark (Fig. 2). Thus, we considered the onset of each call within a series a separate trial (five habituation trials and one test trial per session). In the 'distinct' design, the average difference between calls was 39% of the maximum difference established by the discriminant function analysis; in the 'intermediate' design the average difference was 21%. Calls were spaced by 8 ± 1 s of silence. This is within the range of natural call intervals (Fischer et al. 2001). Within a given experimental session, both the habituation and the test call were recorded from the same adult female. For the five habituation calls, we used three to five different call exemplars, depending on the availability of calls from a given female. Altogether, we assembled 11 different treatments: six series with calls from six females in which the test call was acoustically distinct, and five series from five females in which the test call was acoustically intermediate. We carefully controlled the amplitude of the habituation calls and the test calls, both in terms of the average and the peak amplitude, by adjusting the amplitude of the test call so that, measured at 3 m, it fell within ± 1 dB sound pressure level (re 20 µPa; flat response) of the average of the calls used for habituation. In no case was the test call louder than the loudest call used for habituation (Realistic Sound Level Meter, Radio Shack, Fort Worth, Texas,

U.S.A. (accuracy ± 2 dB (re 20 μPa) at 114 dB (re 20 μPa)).

Because we wanted to ensure that call playbacks did not occur in anomalous contexts, we conducted experiments when the group was relatively widely spread out through a wooded area, where both contact barks and alarm barks have a reasonable probability of occurring (Cheney et al. 1996). Ideally, we would have conducted playbacks only when no previous contact or alarm barks had been heard on that day. However, because contact barks occur at relatively high rates (Cheney et al. 1996) and are heard far more often than alarm barks (Fischer et al. 2001), this was not possible. As a result, we performed playbacks only if neither call type had been heard within the previous half hour. We conducted sessions opportunistically, in contexts that we assessed as relaxed (i.e. no intragroup aggression was ongoing).

When conducting a playback session, we first searched for a potential subject that was sitting at least 3 m from any other group member. The subject was maternally unrelated to the signaller whose call was to be played. After locating the subject, one observer hid a loudspeaker (BOSE Roommate II powered loudspeaker) behind bushes or tall grass, while the other filmed the subject's responses using a SONY Hi8 camcorder CCD-TR750. We scored as responses only head turns of at least approximately 45° towards the speaker (see below). We placed the speaker at approximately right angles to the animal at a mean distance of 18.1 m (range 15–21 m). The playback was initiated when the subject had been looking away from the loudspeaker for at least 10 s, so that no baseline looking time had to be taken into account. We used a SONY DAT TCD-D100 to broadcast calls at a mean (± SD) average amplitude of 56.6 ± 0.9 dB (re 20 μPa; flat) and a mean (± SD) peak amplitude of 60.2 ± 1.6 dB (re 20 μPa; flat) at 20 m. On a calm day, the average background noise was below 50 dB (re 20 μPa; flat). The natural amplitude of contact barks averaged 69 dB (re 20 μPa; flat; range 65–71 dB) at 8–12 m, based on readings from five females. Although we have no amplitude readings for alarm calls, we had the impression that both call types have a similar amplitude. We filmed the behaviour of the subject for approximately 1 min prior to the playback and 20 s thereafter. We also noted the subject's behaviour, as well as date, time, location of the playback, and the number and identity of individuals in the vicinity. Finally, we made a sketch of the location of the speaker and the video camera in relation to the subject. We conducted the habituation experiments between May 1998 and April 1999.

We initially established the criterion of a minimum of three responses (i.e. looking towards the loudspeaker) for an experimental playback session to qualify as valid. Because many subjects failed to respond to the habituation calls (trials 1–5), however, we also included in our analysis the two sessions in which the subject only responded twice during playback (one subject in each condition). Sessions in which the subject showed no apparent response during the first three habituation trials (i.e. trials 1–3) were aborted (15 sessions). In another 13 sessions, we had to stop experimentation because the animal moved away or some other animal approached the subject. We also performed 34 'mock sessions' (see also Palombit et al. 1997) in which we hid the speaker and set up the camera but broadcast no calls. These 'sessions' served to avoid cueing the animals through experimental set-up. Altogether, we conducted 17 experimental playback sessions. In nine sessions, the test call consisted of a harsh alarm bark (distinct condition: $N=5$ male and $N=4$ female subjects), while in eight sessions, the test call was an intermediate alarm bark (intermediate condition: $N=4$ male and $N=4$ female subjects). Neither sex nor placement of the speaker had an influence on the animal's propensity to respond (sex: $\chi_1^2=0.52$, NS; placement of speaker: $\chi_1^2=1.45$, NS).

Single-call experiments

To examine the behavioural responses to calls from the different categories, we conducted a second set of experiments in which we played a single call from each of the four categories: distinct (=typical) and intermediate alarm calls, and typical and intermediate contact calls. Altogether, we conducted 35 experiments on 35 adult subjects, 14 males and 21 females. We used eight different typical alarm calls recorded from five females, seven intermediate alarm calls recorded from six females, six typical contact barks recorded from six females and seven intermediate contact calls recorded from seven females. No single call exemplar was used more than twice. The experimental set-up corresponded to the one described above with the only difference being that instead of a whole series of calls, we played only one call exemplar on any given trial. We conducted these experiments between June 1998 and May 1999.

Data Analysis

We analysed subjects' responses on a frame-by-frame basis using the Adobe Premiere Software 'lite' version 1.4. We first digitized the respective video clips (25 frames/s), assigned a random code to the clips and flagged the onset of the calls. Later, we analysed the recordings blind with respect to the experimental design and with the audio channel turned off. We measured the latency to respond (time between onset of call and onset of response) and scored only responses that occurred within 2 s from the onset of any given call. For data analysis, we measured the response duration as the amount of time spent looking towards the loudspeaker. For statistical analysis of the habituation experiments, we used an exact Wilcoxon matched-pairs signed-ranks test due to the small sample size (Mundry & Fischer 1998). In cases when the values for the last habituation trial and the test trial showed no difference, we followed the suggestions of Bortz et al. (1990) and assigned a positive sign to half of the 'zero differences', and a negative sign to the other half. For statistical analysis of the single-call playbacks, we used a Kruskal–Wallis analysis of variance (ANOVA) by ranks corrected for ties. For pairwise comparisons, we used the outcome of a post hoc test of a one-way ANOVA on the ranked data. All tests were two tailed.
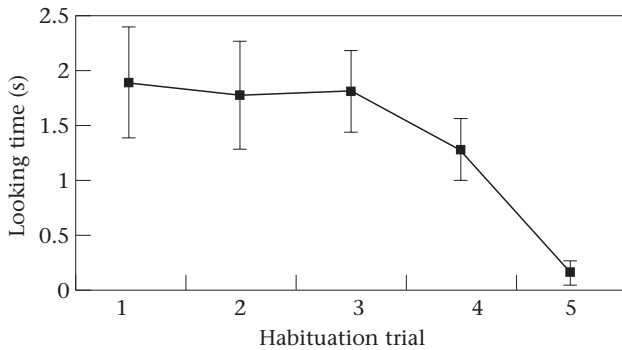
Figure 3. Time spent looking ($\bar{X}\pm$SE) towards the speaker after presentation of the calls used for habituation pooled for all experimental sessions (N=17). Each presentation of a call was spaced by 8±1 s.

RESULTS

Habituation Experiments

Subjects responded to playbacks either by looking towards the speaker or by apparently ignoring the call entirely. In no case did a call playback elicit running towards trees. Figure 3 shows the mean ($\pm$ SD) looking time across both treatments for playback of the five habituation calls. Looking time stayed constant for the first three trials and then dropped to almost zero by playback of the last habituation call. Only two subjects still looked towards the speaker by the fifth trial. The looking time between the first and the fifth habituation trial decreased significantly (exact Wilcoxon matched-pairs signed-ranks test: T=148, N=17, P<0.001), indicating that subjects habituated to the repeated presentation of the same females' contact barks.

Figure 4 presents looking time separately for the two conditions in test trials. When the test call was an intermediate alarm call, there was no significant revival of responses (difference between the response duration of the last habituation trial and the test trial: T=18.5, N=8, NS). However, when the test call was a harsh alarm bark, the subjects showed a significant recovery of their responses (T=43.5, N=9, P=0.012).

Single-call Experiments

Figure 5 shows the looking time after playback of a single exemplar of typical or intermediate contact and alarm barks. Note that the looking time after presentation of a clear contact bark in the habituation and in the single-call experiments reflect two different samples of animals: in the single-call experiments, we included the looking time from all subjects tested, irrespective of whether they had responded or not. In the habituation experiments, we only considered the looking times of animals that had responded at least three times.

In the single-call experiments, animals did not show any overt responses after playback of clear contact barks, intermediate contact barks, or intermediate alarm barks. Only harsh alarm barks reliably elicited responses. Responses differed significantly in relation to the call
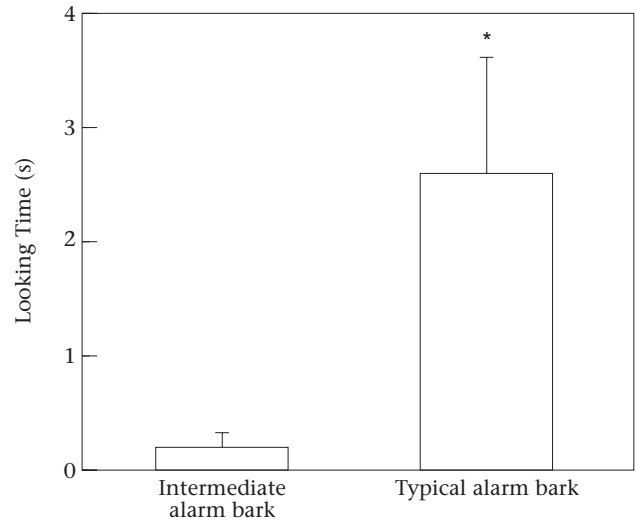

Figure 4. Time spent looking ($\bar{X}\pm$SE) towards the speaker after presentation of the test calls after playback of an intermediate alarm bark, and after playback of a typical alarm bark. An asterisk (*) indicates a significant differences between responses in the test trial versus the last habituation trial.
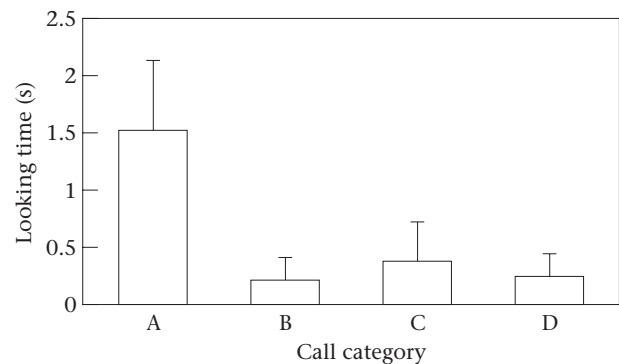

Figure 5. Time spent looking ($\bar{X}\pm$SE) towards the speaker after presentation of single exemplars of baboons barks. A: Typical alarm barks; B: intermediate alarm barks; C: intermediate contact barks; D: typical contact barks.

presented (Kruskal–Wallis test, corrected for ties: χ^2_3=9.75, P<0.05). Post hoc multiple comparisons (Bonferroni correction) revealed significant or marginally significant differences between responses to harsh alarm barks and all other categories (intermediate alarm barks: P=0.035; intermediate contact barks: P=0.068; clear contact barks: P=0.038), but no significant differences between any other pair.

DISCUSSION

In the habituation experiments, baboons showed a clear recovery of response after playback of a harsh alarm bark. Contrary to our expectations, however, subjects showed no such recovery when played intermediate alarm barks. Apparently, they generalized from contact barks to intermediate variants of alarm barks. We first hypothesized that this might have occurred because the repeated

playback of clear contact barks provides a natural context in which intermediate variants of barks occur. Results from playbacks of single exemplars, however, forced us to reject this explanation.

From our results, we are unable to determine why the baboons failed to distinguish between clear contact barks and intermediate alarm barks. One possibility is that subjects were in fact unable to distinguish between these bark variants. Alternatively, the perceived difference might not have been meaningful to them (Nelson & Marler 1990). However, playbacks with infant baboons (Fischer et al. 2000) have shown that infants do discriminate between intermediate alarm barks and clear contact barks, suggesting that adults' apparent lack of discrimination between these call variants is not due to an inability to do so, but rather to a lack of motivation. In other words, they do perceive a meaningful difference between these bark variants, but the message conveyed in the intermediate bark does not warrant any action.

It seems surprising that baboons failed to respond to intermediate alarm barks despite high levels of predation in this population. Given the low costs of a simple head-turning response, we would have expected that baboons would be more likely to overgeneralize from alarm barks to intermediate contact barks, and respond strongly to all but the clear contact bark variants. Playbacks of alarm calls elicit overt antipredator behaviour in other primate species (e.g. vervet monkeys: Seyfarth et al. 1980; captive lemurs *Lemur catta*: Pereira & Macedonia 1991; captive Barbary macaques: Fischer et al. 1995; Diana monkeys, *C. diana*: Zuberbühler et al. 1999). We find it difficult to explain why these baboons are apparently so different, both in terms of their inclination to respond and in their response strength.

One possibility is that the baboons' propensity to respond to alarm barks depends as much on the context in which the call is given as on the call's acoustic features. Studies of several nonhuman primate species have now demonstrated that listeners' responses are influenced by a number of variables, including context (Rendall et al. 1999; Macedonia & Evans 1993), caller identity (Seyfarth & Cheney 1984; Rendall et al. 1996, 1999; Cheney & Seyfarth 1997, 1999; Palombit et al. 1997; Hammerschmidt & Fischer 1998), and perceived risk (Zuberbühler et al. 1999; Zuberbühler 2000). The experiments described here were always conducted in contexts that did not appear to present an immediate danger. Baboons might be more likely to respond to intermediate barks in areas where they are more vulnerable to predation. Unfortunately, we were unable to perform playback experiments under conditions of high putative risk, either because the animals were travelling too fast or because visibility was so poor that we were not able to film the subject's behaviour.

The results of these experiments seem difficult to reconcile with those obtained in the earlier study of Barbary macaques (Fischer 1998). One important difference in the Barbary macaque study was that playbacks involved two different alarm call types that were equally common and equally likely to elicit a response. Perhaps as a result, responses depended mainly on the acoustic properties of the calls. Baboons, in contrast, were asked to discriminate among call types that were asymmetrical in both their baseline frequencies and the likelihood that they would elicit a response. Under natural conditions, contact barks occur at high rates and elicit almost no response from unrelated listeners, whereas alarm barks occur rarely and elicit a strong response. Perhaps a naturally high baseline rate of contact barks causes listeners to ignore all barks that do not fall unambiguously into the alarm category. However, the propensity to respond may vary in relation to perceived risk. Future research should address in more detail the integration of different factors that govern behavioural responses to vocalizations in nonhuman primates.

References

Bortz, J., Lienert, G. A. & Boehnke, K. 1990. *Verteilungsfreie Methoden in der Biostatistik*. Berlin: Springer.

Byrne, R. W. 1981. Distance vocalisations of Guinea baboons (*Papio papio*) in Senegal: an analysis of function. *Behaviour*, **78**, 283–313.

Cheney, D. L. & Seyfarth, R. M. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, **36**, 477–486.

Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys see the World*. Chicago: University of Chicago Press.

Cheney, D. L. & Seyfarth, R. M. 1997. Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour*, **54**, 409–418.

Cheney, D. L. & Seyfarth, R. M. 1999. Recognition of other individuals' social relationships by female baboons. *Animal Behaviour*, **58**, 67–75.

Cheney, D. L., Seyfarth, R. M. & Palombit, R. 1996. The function and mechanisms underlying baboon 'contact' barks. *Animal Behaviour*, **52**, 507–518.

Fischer, J. 1998. Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, **55**, 799–807.

Fischer, J., Hammerschmidt, K. & Todt, D. 1995. Factors affecting acoustic variation in Barbary macaque (*Macaca sylvanus*) disturbance calls. *Ethology*, **101**, 51–66.

Fischer, J., Cheney, D. L. & Seyfarth, R. M. 2000. Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London, Series B*, **267**, 2317–2321.

Fischer, J., Hammerschmidt, K., Cheney, D. L. & Seyfarth, R. M. 2001. Acoustic features of female chacma baboon barks. *Ethology*, **107**, 33–54.

Gouzoules, H. & Gouzoules, S. 1989. Design features and developmental modification of pigtail macaque, *Macaca nemestrina*, agonistic screams. *Animal Behaviour*, **37**, 383–401.

Hall, K. R. L. & DeVore, I. 1965. Baboon social behaviour. In: *Primate Behaviour: Field Studies of Monkeys and Apes* (Ed. by I. DeVore), pp. 53–110. New York: Holt, Rinehart & Winston.

Hamilton, W. J., Buskirk, R. E. & Buskirk, W. H. 1976. Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. *Ecology*, **57**, 1264–1272.

Hammerschmidt, K. & Fischer, J. 1998. Maternal discrimination of offspring vocalizations in Barbary macaques (*Macaca sylvanus*). *Primates*, **39**, 231–236.

Hauser, M. D. 1991. Sources of acoustic variation in rhesus macaque (*Macaca mulatta*) vocalizations. *Ethology*, **89**, 29–46.

Hauser, M. D. 1996. *The Evolution of Communication*. Cambridge, Massachusetts: MIT Press.

Hauser, M. D. 1998. Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour*, **55**, 1647–1658.

Hauser, M. D. & Marler, P. 1993. Food-associated calls in rhesus macaques (*Macaca mulatta*). 1. Socioecological factors. *Behavioural Ecology*, **4**, 194–205.

Macedonia, J. M. & Evans, C. S. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93**, 177–197.

Marler, P. 1975. On the origin of speech from animal sounds. In: *The Role of Speech in Language* (Ed. by J. F. Kavanaugh & J. E. Cutting), pp. 11–37. Cambridge, Massachusetts: MIT Press.

Marler, P. 1976. Social organization, communication and graded signals: the chimpanzee and the gorilla. In: *Growing Points in Ethology* (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 239–280. Cambridge: Cambridge University Press.

Marler, P., Evans, C. S. & Hauser, M. D. 1992. Animal signals: motivational, referential, or both? In: *Nonverbal Vocal Communication* (Ed. by H. Papoušek, U. Jürgens & M. Papoušek), pp. 66–86. Cambridge: Cambridge University Press.

Mitani, J. C. 1996. Comparative studies of African ape vocal behaviour. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 241–254. Cambridge: Cambridge University Press.

Mundry, R. & Fischer, J. 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect *P* values: examples from *Animal Behaviour*. *Animal Behaviour*, **56**, 256–259.

Nelson, D. A. & Marler, P. 1990. The perception of birdsong and an ecological concept of signal space. In: *Comparative Perception. Vol. 2: Complex Signals* (Ed. by W. C. Stebbins & M. A. Berkley), pp. 443–478. New York: J. Wiley.

Palombit, R. A., Seyfarth, R. M. & Cheney, D. L. 1997. The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour*, **54**, 599–614.

Pereira, M. E. & Macedonia, J. M. 1991. Ringtailed lemur antipredator calls denote predator class, not response urgency. *Animal Behaviour*, **41**, 543–544.

Pola, Y. V. & Snowdon, C. T. 1975. The vocalizations of pygmy marmosets, *Cebuella pygmaea*. *Animal Behaviour*, **23**, 826–846.

Rendall, D., Rodman, P. S. & Emond, R. E. 1996. Vocal recognition of individuals and kin in free ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.

Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. 1999. The meaning and function of grunt variants in baboons. *Animal Behaviour*, **57**, 583–592.

Rendall, D., Cheney, D. L. & Seyfarth, R. M. 2000. Proximate factors mediating 'contact' calls in adult female baboons and their infants. *Journal of Comparative Psychology*, **114**, 36–46.

Ross, K. 1987. *Okavango: Jewel of the Kalahari*. New York: Macmillan.

Seyfarth, R. M. & Cheney, D. L. 1984. The acoustic features of vervet monkey grunts. *Journal of the Acoustical Society of America*, **75**, 1623–1628.

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.

Snowdon, C. T. & Pola, Y. V. 1978. Interspecific and intraspecific responses to synthezised pygmy marmoset vocalizations. *Animal Behaviour*, **26**, 192–206.

Wyttenbach, R. A. & Hoy, R. R. 2000. Categorical perception of behaviourally relevant stimuli by crickets. In: *The Design of Animal Communication* (Ed. by M. D. Hauser & M. Konishi), pp. 559–576. Cambridge, Massachusetts: MIT Press.

Zuberbühler, K. 2000. Causal knowledge of predator's behaviour in wild Diana monkeys. *Animal Behaviour*, **59**, 209–220.

Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. 1999. Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, **113**, 33–42.