Interspecies semantic communication in two forest primates

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West African Diana monkeys (*Cercopithecus diana*) and Campbell's monkeys (*Cercopithecus campbelli*) frequently form mixed-species associations. Males of both species produce acoustically distinct alarm calls to crowned eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*), two of their main predators. Field playback experiments were conducted to investigate whether Diana monkeys respond to Campbell's alarm calls and whether they understand the calls' semantic content. Diana monkeys responded to playback of Campbell's leopard or eagle alarm calls as though the original predator were present. In a second experiment, Diana monkeys were primed with either Campbell's eagle or leopard alarm calls and then subsequently probed with the vocalizations of a crowned eagle or a leopard. Results showed that monkeys used the semantic information conveyed by the Campbell's alarm calls to predict the presence of a predator. The data are consistent with the hypothesis that non-human primates are able to use acoustic signals of diverse origin as labels for underlying mental representations.

Keywords: alarm call; anti-predator behaviour; non-human primate; semantic communication; mixed species

1. INTRODUCTION

In the Taï forest of Côte d'Ivoire, Diana monkeys (*Cercopithecus diana*) and Campbell's monkeys (*Cercopithecus campbelli*) frequently associate in mixed-species groups, presumably to improve their protection against predation (Noë & Bshary 1997). Both species live in small social groups, consisting of one adult male and several adult females with their offspring. Males of both species produce acoustically different alarm calls to leopards and crowned eagles (Zuberbühler *et al.* 1997; Zuberbühler 2000a, fig. 2), two of their main predators. Pilot observation suggested that both species respond to each other's alarm calls. Although interspecific responses in primates have been known for some time (e.g. Struhsaker 1970, p. 379), it has never been empirically investigated whether they are in fact elicited by alarm calls as opposed to, for example, escape behaviour. Moreover, if alarm calls are crucial in interspecies communication, then it is of interest whether recipients simply respond to the acoustic features of the other species' alarm calls or whether their response is based on an understanding of the calls' meaning.

Previous studies on interspecies communication in primates come from two main sources. First, vervet monkeys (*Cercopithecus aethiops*) respond to alarm calls of superb starlings (*Spreo superbus*), which produce a 'terrestrial alarm' to a wide variety of ground predators and a 'raptor alarm' to predators that attack from the air. Playback experiments were consistent with the hypothesis that vervet monkeys attended to the meaning of the starlings' alarm calls (Seyfarth & Cheney 1990). Second, both Verreaux's sifakas (*Propithecus verreauxi*) and ring-tailed lemurs (*Lemur catta*) produce acoustically different alarm calls to raptors and carnivores. Free-ranging ring-tailed

lemurs responded appropriately not only to their own alarm calls but also to playbacks of the alarm calls of sympatric sifakas. Interestingly, however, when sifakas' raptor alarms were played to captive ring-tailed lemurs, which had never heard these calls before, individuals still responded appropriately by looking into the sky, suggesting that perhaps ring-tailed lemurs responded to shared acoustic features in both species' alarm calls, rather than to the associated meaning (Oda & Masataka 1996).

When Diana monkeys hear the growls of a leopard they respond by giving numerous alert calls, leopard alarm calls, and occasionally approaching the predator (Zuberbühler *et al.* 1999b). If monkeys hear leopard growls for a second time from the same location, however, their vocal response is very weak, presumably because the costs of alarm calling now outweigh the benefits: conspecifics and the predator are warned and continuous alarm calling would only attract other predators (e.g. chimpanzees) to the site. However, alarm calls have the same priming effect as predator vocalizations: Diana monkeys primed with conspecific alarm calls no longer respond to the predator the alarm calls refer to. For example, monkeys primed with the alarm calls conspecific males give to leopards no longer respond to leopard growls, even though growls normally elicit a strong response. These results were consistent with the hypothesis that, when hearing a conspecific's alarm calls, Diana monkeys form a mental representation of the corresponding predator, which allows them to respond as if they already knew of its presence (Zuberbühler *et al.* 1999a).

The present study extends this approach by investigating Diana monkeys' understanding of another species' alarm calls. Two sets of experiments were conducted to investigate whether Diana monkeys respond to Campbell's alarm calls and whether their responses are based on an understanding of the calls' semantic content.

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2. METHODS

(a) *Study site*

Field playback experiments and observations were conducted in the Taï National Park, Côte d'Ivoire, between June 1996 and February 1999 in a study area of approximately $50\,km^2$ of primary rain forest ($5°50'$ N, $7°21'$ W).

(b) *Data collection*

In conducting playback experiments, I systematically searched the study area until I located a wild Diana monkey group, typically by hearing their vocalizations. I noted their geographical location with a map and a Magellan Pioneer Global Positioning System® receiver and monitored their vocal behaviour. If I was confident that no monkey had detected me, I initiated a playback trial by positioning the speaker at about 2 m from the ground at a distance of about 50 m, outside the group's visual range. I started tape-recording the subjects' vocal response about 5 min before the first playback stimulus. Playback stimuli were broadcast with a Sony WMD6C® Professional Walkman connected to a Nagra DSM® speaker–amplifier. Vocalizations were tape-recorded with a Sony TCM5000EV® recorder and a Sennheiser ME88® or ME67® directional microphone. Stimulus intensities were measured with a Radio Shack sound-level meter 33-2050®, C-weighting, at 1 m distance from the speaker. Spectrograms were made with the software package Canary 1.2.

(c) *Playback stimuli*

I simulated the predator presence by playing back predator vocalizations in the vicinity of a monkey group. This was either a 15 s recording of shrieks of a crowned eagle, recorded in the study area, or a 15 s recording of growls of a leopard, obtained from the National Sound Archive, London, UK. Previous studies had shown that monkeys responded to recordings of predator vocalizations as if the real predator were present (e.g. Hauser & Wrangham 1990). Vocalizations were played back in the following amplitude range: leopard growls, 88–100 dB; crowned eagle shrieks, 90–110 dB; Campbell's alarm calls, 90–100 dB. Within these naturally sounding ranges, intensity had no effect on the vocal response of Diana monkeys (K. Zuberbühler, unpublished data).

(d) *Dependent variables*

The dependent variables in all trials were the number of vocalizations jointly produced by the focal Diana monkey group. Because I was working with unhabituated groups, it was not possible to sample at the individual level or to count the number of individuals per group. Hence, each trial represents the combined vocal response of several adult females with their offspring. Adult females, subadults, and juveniles account for most of the vocal activity in a group. They are responsible for the following vocalizations, which can be distinguished by ear: the contact call, typically given in non-predatory contexts; the alert call, typically given after a variety of disturbances or after detection of predators; the leopard alarm call, given by adult females after detection of a leopard; the eagle alarm call, given by adult females in response to crowned eagles; and other call types, such as trills, agonistic calls, or intergroup calls. Leopard and eagle alarm calls are usually produced by two to three adult females in the group, minimizing the effect of potential differences in group size. The single adult male of the group did not produce any of the vocalizations described above. Instead, males restricted their vocal communication to loud alarm calls, given in response to predators or after other disturbances, such as falling trees. The males' calling behaviour, including spectrograms, is described elsewhere (Zuberbühler 2000*b*).

(e) *Pseudoreplication*

The home ranges of Diana and Campbell's monkey groups are relatively small and stable over time (about $0.8\,km^2$ per group) with significant overlap between species (Höner *et al.* 1997; R. Noë, unpublished data). I obtained statistical independence by testing a large number of different Diana monkey groups throughout the $50\,km^2$ area, such that each group heard a particular stimulus or stimulus pair only once. To maximize further the external validity of the results one might ideally have played different exemplars of each stimulus class in every trial. The number of available master recordings, however, prevented me from doing so. In Diana monkeys, real predators elicit the same vocal behaviour, both quantitatively and qualitatively, as do the recordings of their vocalizations (K. Zuberhubühler, unpublished data), indicating that a small number of good recordings can usefully represent the different predator classes.

(f) *Experiment 1: do Diana monkeys respond to Campbell's alarm calls?*

In the first experiment, I compared Diana monkeys' responses to Campbell's alarm calls with their responses to predator vocalizations. As playback stimuli, I used recordings from four different Campbell's males: two series of alarm calls given to a playback of crowned eagle shrieks (henceforth 'Campbell's eagle alarm calls'), two others given to a playback of leopard growls (henceforth 'Campbell's leopard alarm calls').

Campbell's eagle alarm calls are often given in rapid series whereas leopard alarm calls are typically given with longer intercall intervals. The playback tapes of Campbell's alarm calls were edited such that I controlled for either (i) the number of calls, i.e. seven leopard alarm calls over 15 s or seven eagle alarm calls over 12 s, or (ii) duration of exposure, i.e. nine eagle alarm calls over 5 s or four leopard alarm calls over 5 s ($n = 6$ Diana monkey groups for all treatments except for the last in which $n = 8$). Finally, I recorded responses to a 15 s playback of leopard growls ($n = 16$ Diana monkey groups) and a 15 s playback of crowned eagle shrieks ($n = 17$ Diana monkey groups). Using non-parametric statistics, I compared the Diana monkeys' vocal behaviour across the four stimulus types.

(g) *Experiment 2: do Diana monkeys understand the meaning of Campbell's alarm calls?*

In the second experiment, I investigated whether Diana monkeys were able to attend to the meaning of Campbell's alarm calls. In this experiment, a Diana monkey group heard two playback stimuli, a prime and a probe, separated by 5 min silence. The acoustic features of the two stimuli always changed while the semantic features either did or did not change. Subjects heard Campbell's alarm calls followed, after 5 min silence, by eagle shrieks or leopard growls. If monkeys understand the meaning of the alarm calls, then they should respond weakly to the predator in cases where they have been primed with the corresponding alarm calls (for the same reasons they respond weakly if the same predator is presented twice). They should respond strongly to the predator in cases where they have been primed with the non-corresponding predator because in this case the monkeys cannot use the alarm calls to
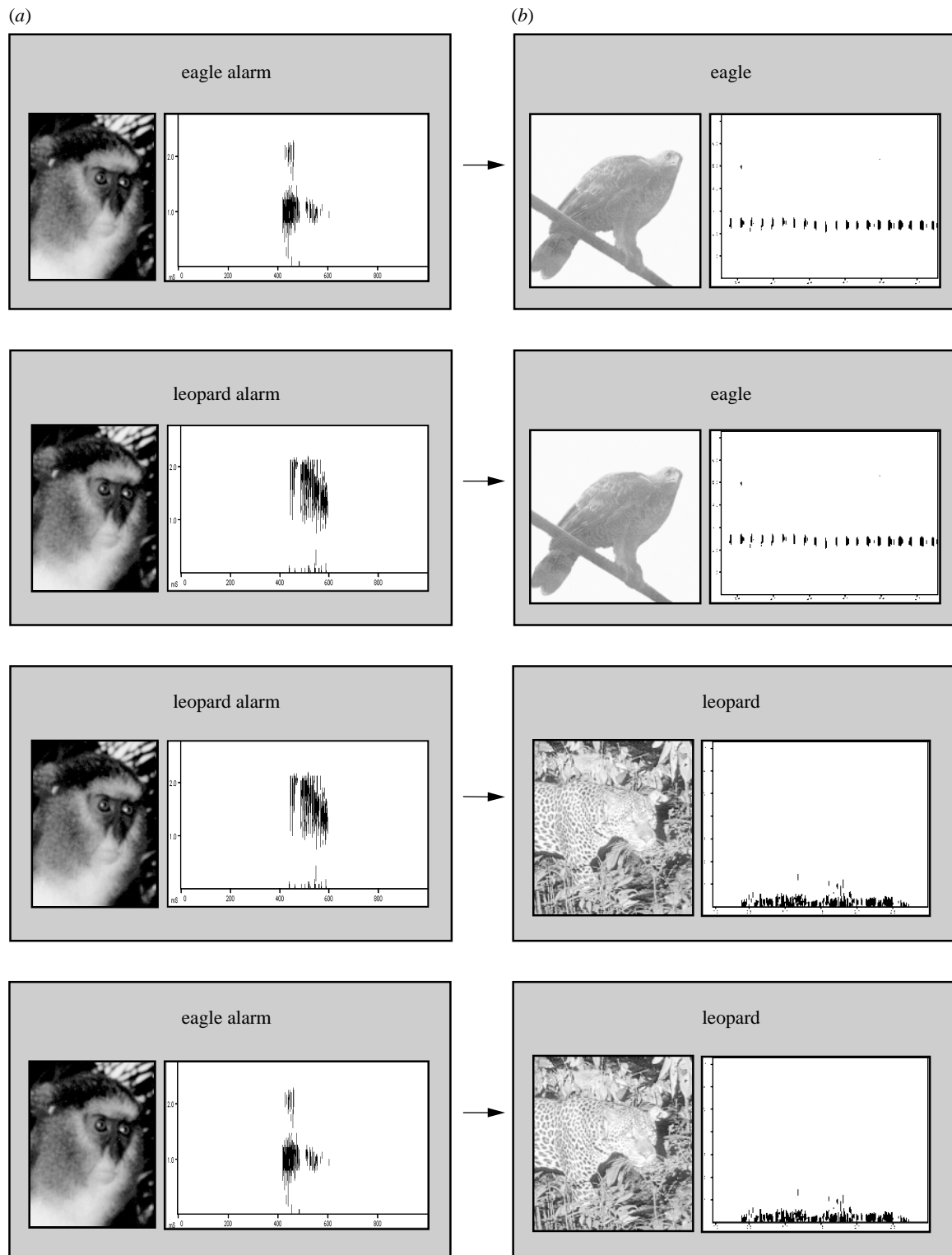
(a)

(b)

Figure 1. Design of the prime–probe experiment. (Photograph of leopard: David Jenny.) (*a*) Prime, Campbell's alarm calls (*b*) probe, predator vocalizations.

predict its presence. Statistical analysis should reveal that responses to the predator are significantly weaker in groups primed with the corresponding alarm calls than those primed with the non-corresponding alarm calls, the dependent variables being the number of leopard and eagle alarm calls given by female Diana monkeys. Non-parametric statistics were used to compare differences in call rates to the probes as a function of the priming history. Figure 1 illustrates the experimental design.

3. RESULTS

(a) *Experiment 1: do Diana monkeys respond to Campbell's alarm calls?*

Diana females gave acoustically different alarm calls to different playback stimuli. Playbacks of eagle shrieks and Campbell's eagle alarm calls usually caused the Diana monkeys to give eagle alarm calls, some contact calls and a few alert calls, but no leopard alarm calls. Playbacks of
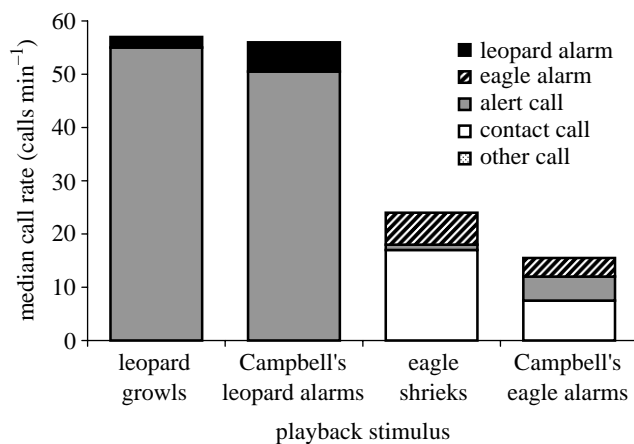
Figure 2. Vocal behaviour of the females in Diana monkey groups after hearing vocalizations of a leopard ($n = 16$), a crowned eagle ($n = 17$), or Campbell's alarm calls to leopard ($n = 14$) or crowned eagle ($n = 12$).

leopards and Campbell's leopard alarm call, in contrast, usually caused the monkeys to give leopard alarm calls and a large number of alert calls, but no eagle alarm calls.

The number of Campbell's alarm calls used in playbacks did not affect the Dianas' responses. There were significant differences neither in the number of Diana eagle alarm calls to five or nine Campbell's eagle alarm calls (Mann–Whitney U-test, two-tailed, $n_1 = n_2 = 6$, $U = 15.5$, $p > 0.35$), nor in the number of Diana leopard alarm calls to four or five Campbell's leopard alarm calls (Mann–Whitney U-test, two-tailed, $n_1 = 6$, $n_2 = 8$, $U = 21.5$, $p > 0.38$). Hence, data were pooled and are plotted in figure 2. Similarly, presence or absence of Campbell's monkeys during a playback experiment did not affect the vocal response of Diana monkeys. There were no significant differences in the number of Diana eagle alarm calls (Mann–Whitney U-test, two-tailed, $n_1 = 5$, $n_2 = 7$, $U = 17.5$, $p > 0.5$) or leopard alarm calls (Mann–Whitney U-test, two-tailed, $n_1 = 8$, $n_2 = 6$, $U = 19.0$, $p > 0.28$) depending on whether or not Campbell's monkeys were present.

Because Diana eagle and leopard alarm calls are most critical for this hypothesis, I analysed, for each trial, whether or not at least one of these calls occurred in each group. Using Fisher's exact probability tests, I tested the null hypothesis that the utterance of one or more alarm calls of each type was independent of the playback stimulus. Diana monkey females were significantly more likely to give leopard alarms when hearing leopard growls than eagle shrieks ($p < 0.001$) or Campbell's eagle alarms ($p < 0.002$). They also were significantly more likely to give leopard alarms when hearing Campbell's leopard alarms than eagle shrieks ($p < 0.001$) or Campbell's eagle alarms ($p < 0.001$) and significantly more likely to give eagle alarms when hearing eagle shrieks than leopard growls ($p < 0.001$) or Campbell's leopard alarms ($p < 0.001$). They also were significantly more likely to give eagle alarms when hearing Campbell's eagle alarms than leopard growls ($p < 0.001$) or Campbell's leopard alarms ($p < 0.001$). There was no significant difference, however, in the occurrence of female eagle

alarms after hearing eagle shrieks or Campbell's eagle alarms ($p > 0.16$). Similarly, there was no statistical difference in the occurrence of female leopard alarms after hearing leopard growls or Campbell's leopard alarms ($p > 0.19$).

(b) Experiment 2: do Diana monkeys understand the meaning of Campbell's alarm calls?

Twelve Diana groups heard Campbell's eagle alarm calls followed by eagle shrieks. The Diana monkeys responded weakly to eagle shrieks, even though this stimulus was highly effective in eliciting eagle alarm calls under unprimed conditions (figures 2 and 3). In the next series, seven Diana monkey groups heard Campbell's leopard calls followed by eagle shrieks. Diana monkey groups responded strongly to eagle shrieks even though they had just responded strongly to Campbell's leopard alarm calls. As predicted, Diana monkeys produced significantly fewer eagle alarm calls to eagle shrieks when primed with the Campbell's eagle alarms than when primed with leopard alarm calls (Mann–Whitney U-test, one-tailed; $n_1 = 7$; $n_2 = 12$; $U = 21$; $p < 0.05$; figure 3).

In the analogous case, 11 Diana groups heard male Campbell's leopard alarm calls followed by leopard growls. The Diana monkeys responded weakly to playbacks of leopard growls even though this stimulus is normally highly effective in eliciting leopard alarm calls (figures 2 and 3). In the final series, 12 Diana groups heard Campbell's eagle alarm calls followed by leopard growls. Diana monkeys responded strongly to leopard growls, even though they had just responded strongly to Campbell's eagle alarm calls. As predicted, Diana monkeys produced significantly fewer leopard alarm calls to leopard growls when primed with Campbell's leopard alarm calls than when primed with eagle alarm calls (Mann–Whitney U-test, one-tailed; $n_1 = 11$; $n_2 = 12$; $U = 26.5$; $p < 0.03$; figure 3).

4. DISCUSSION

Male Campbell's monkeys produce two acoustically different alarm calls to crowned eagles and leopards (figure 1). Diana monkeys, which often associate with Campbell's monkeys, are sensitive to these acoustic differences and respond to them as if the corresponding predator were present (figure 2). This finding is highly relevant for the hypothesis that predation pressure is the ultimate cause for the formation of mixed-species associations (e.g. Noë & Bshary 1997). So far, it has only been an implicit assumption that members of mixed-species groups understand each other's alarm calls and hence profit from improved predator detection. The present study provides the first empirical evidence showing that alarm calls produced by heterospecifics are indeed equally effective in inducing anti-predator behaviour as the alarm calls of conspecifics.

When responding to Campbell's alarm calls, Diana monkeys do not simply attend to the acoustic features of the other species' alarm calls but to the calls' semantic content. This is because subjects responded weakly to predator vocalizations but only if they were primed with the corresponding alarm calls of the Campbell's monkey (figure 3). Priming with the non-corresponding alarm
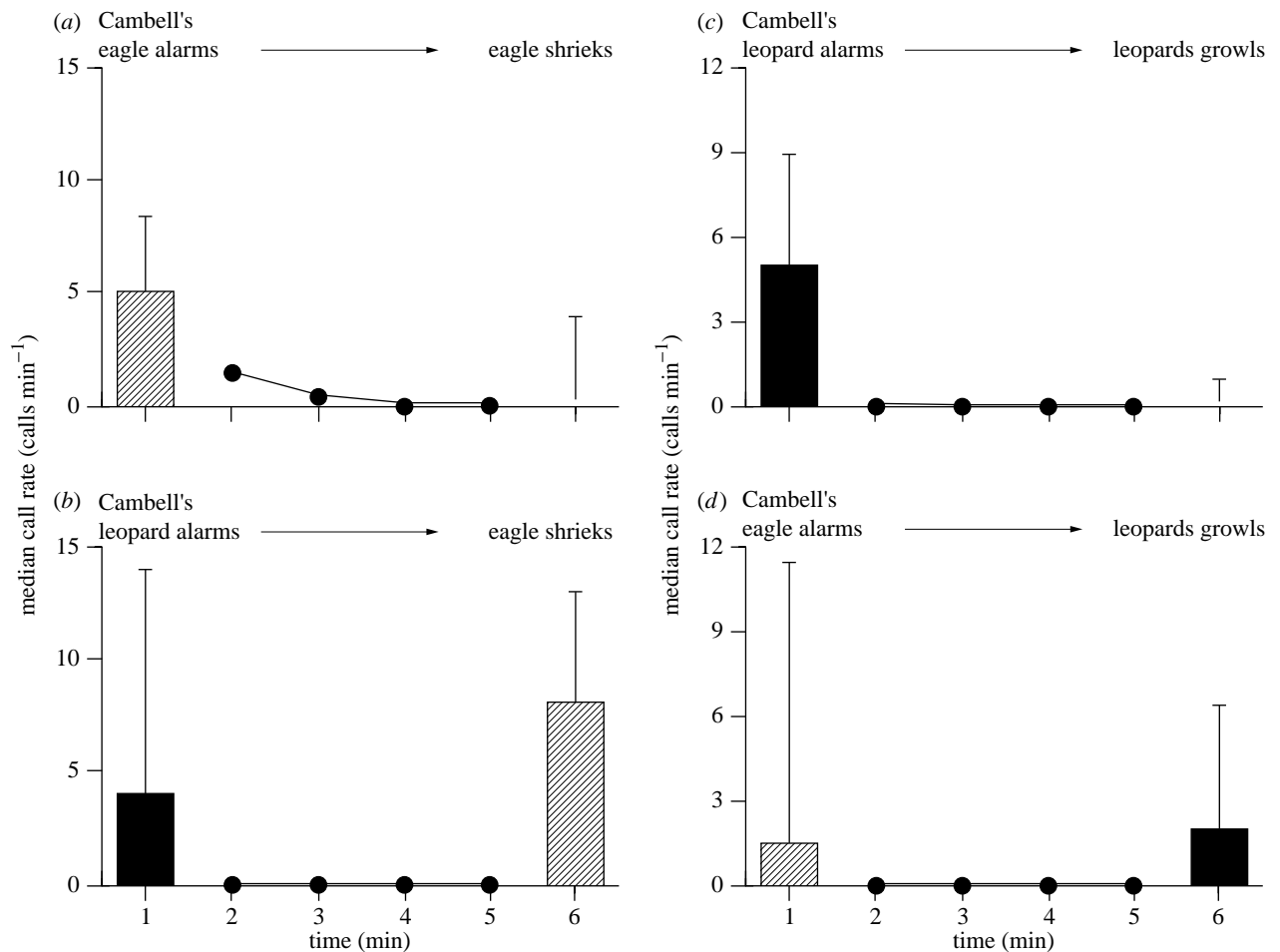
Figure 3. Vocal responses of Diana monkeys to predators after being primed with either Campbell's eagle or leopard alarm calls (median number of calls and third quartile). For clarity reasons, only eagle and leopard alarm call rates are plotted here. Solid bars, female leopard alarm calls; striped bars, female eagle alarm calls.

calls did not have such an effect, suggesting that Diana monkeys use the Campbell's alarm calls as labels for the same underlying representations of the different predator classes. These data are analogous to previous studies where Diana monkeys' responses to their own alarm calls were investigated (Zuberbühler *et al.* 1999*a*), indicating that Diana monkeys can flexibly use and assess information derived from the communication of other species (Zuberbühler 2000*c*,*d*).

In some animal species, particular vocalizations provide nearby listeners with information about some object or event—like a predator, food or another group—that is physically separate from the calling individual. Because these vocalizations appear to refer to the environmental events that elicit them they have been termed semantic (Seyfarth *et al.* 1980), thus challenging the notion of animal vocalizations as purely emotional displays (Marler *et al.* 1992). Examples of natural semantic communication in primates come from studies on the alarm call behaviour of vervet monkeys (Seyfarth *et al.* 1980) and ring-tailed lemurs (Pereira & Macedonia 1991), but functionally referential alarm calls have also been reported in some non-primate species (e.g. Hauser 1996). These and a number of studies from psychological laboratories (e.g. Pepperberg 1990) suggest that the necessary cognitive competence for understanding meaning

may not be restricted to humans and their linguistic abilities. From the perspective of the signaller, however, primate vocalizations may differ significantly from human language. Non-human primates seem to have little flexibility in assigning calls to contexts and, more importantly, seem unable to incorporate new calls into their repertoire (e.g. Cheney & Seyfarth 1998). Equally important, non-human primates do not seem to vocalize in order to affect a recipient's mental state, a typical feature of human linguistic behaviour. It has been argued that the reason for this is that primates are unable to or have great difficulty in understanding each other as mental agents (Tomasello & Call 1997, p. 384), an essential prerequisite for intentionally communicating meaning. From the perspective of the call recipient, however, the difference between primate alarm calls and human linguistic utterances are less explicit. In this and other studies (e.g. Hauser 1998), it was the meaning of the stimuli, but not the acoustic features that explained the subjects' response patterns. These results extend this finding beyond intraspecific communication by showing that semantic understanding can be based on arbitrary signals, as it is the case for word meaning.

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