

## Original Article

## Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls

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The extent to which animal vocalizations convey specific information about events in the environment is subject to continued debate. The alarm-calls of vervet monkeys have played a pivotal role in this debate as they represent the classic example of a predator-specific call production system combined with a set of equally specific responses by receivers. Here, we revisit the vervet alarm-calling system, and assess the hypothesis that these acoustically distinct calls trigger context- and predator-appropriate behavior. We investigated responses in 2 groups of free-ranging vervet monkeys (*Chlorocebus pygerythrus*) to both natural encounters with predators and experimental presentations of aerial and terrestrial predator alarm calls. Our results show that the modal natural and experimental response was not to initiate escape behavior, either immediately or in the 10s following an alarm call, but to look at the sound source. When monkeys did take evasive action, contextually inappropriate behavior (i.e., behavior that was not appropriate for evading the specific predator type) was as likely to occur as contextually appropriate behavior. The distance at which calls were heard was negatively correlated with the probability of evasive action. Larger group size, and the greater mean distance at which natural calls were heard, may explain why our animals displayed less predator-appropriate evasion or vigilance than expected. We conclude that the broader social and ecological framework in which calls occur, rather than a simple contextually regular linkage between call types and specific predators, shapes animals' responses to calls in this species.

**Key words:** *Chlorocebus pygerythrus*, playback experiments, vocalizations, predation risk, group size, referential.

## INTRODUCTION

In the field of animal vocal communication, there is ongoing debate over whether animal calls contain meaningful information (see e.g., Hauser 1996; Rendall et al. 2009; Bradbury and Vehrencamp 2011; Seyfarth and Cheney 2013). In the classic early studies of primate alarm calling, it was suggested that calls contained semantic meaning, and could be considered “language-like”; that is, calls were argued to contain information that referred expressly to objects and events in the environment and did not merely reflect some aspect of the animal's internal state (Seyfarth et al. 1980a,b). The acoustic structure of a call was therefore considered to be “arbitrary” in much the same way that the human word for “table” is arbitrary: there is nothing in the sound of the word “table” that is relevant to understanding what a table is, or that conveys some inherent aspect of “tableness.”

An alternative view, put forward around the same time, was that the specific acoustic structure of calls produced by birds and mammals was, in fact, relevant to understanding how and why such calls

were used in particular contexts. That is, it was argued that there existed a consistent, predictable relationship between the structure of a particular sound and the motivation underlying its use. These relationships were termed “motivation-structural” rules by Morton (1977). For example, aggressive contexts tend to be associated with harsh, low-frequency sounds, which are inherently more aversive than sounds used in affiliative contexts (Morton 1977; Owings and Morton 1998). In this view, calls do not contain information about events in the world, and hence do not convey any form of semantic meaning.

As studies accumulated, particularly on the primates, it became apparent that the structure of calls was not as arbitrary as initially thought, but instead showed evidence of the kinds of motivation-structural rules suggested by Morton (1977), which called into question the idea that calls were arbitrary symbols like human words (see Wheeler and Fischer 2012 for a review). Call production was also shown to be rather inflexible, with no experience required to produce each species-specific call, a finding that also raised questions concerning the arbitrariness of vocalizations: if calls referred to external objects and events (their “referents”) in an arbitrary way, with no direct link to acoustic structure, then one

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would expect more variability in how call types were used within and between species. One would also expect to find evidence that calls would have to be learned in order to be recognized and used appropriately (see Wheeler and Fischer 2012 for review).

As a result of findings like these, there was a shift in terminology: calls were now considered to be “functionally referential” (Marler et al. 1992). That is, calls were treated “as if” they contained information for perceivers, but with no claims made about the precise nature of this information, nor any requirement to specify the precise nature of the psychological mechanisms that underpinned the perceivers’ responses. Instead, functional reference required only that a call was reliably elicited by a particular class of stimuli (“context specificity”), and that such calls reliably led to a response that was adaptive for a given stimulus, even when the stimulus was not present (“stimulus independence”) (Scarantino 2010; Wheeler and Fischer 2012). This notion of functional reference has since been applied widely across both mammalian and avian species (Wheeler and Fischer 2012).

Some authors have criticized this idea of functional reference, however, on both conceptual and empirical grounds (e.g., Owren and Rendall 2001; Rendall et al. 2009). Specifically, these authors argue that by continuing to use the term “information,” in a rather loose, metaphorical way, it remains conflated with linguistic notions of “meaning” and so encourages a view of animal vocalizations that is more language-like than is warranted. As an alternative to functional reference, Owren and Rendall (2001) have proposed an “affect conditioning” or “affect induction” model that eliminates any reference to language-like metaphors. This draws on Morton’s (1977) early work on motivation-structural rules, as well as Owings and Morton’s (1998) subsequent “assessment-management” approach to animal vocal communication. Owren and Rendall (2001) suggest that animals learn to associate particular calls with particular contexts by a process of classical conditioning, whereby the acoustic structure of the call taps directly into low-level perceptual, attentional, and motivational processes of perceivers. Animals then learn that these inherently arousing calls predict a particular sequence of events (Owren and Rendall 2001).

As Scarantino (2010) has argued, however, it remains possible to distinguish carefully between “natural meaning” (i.e., instances where calls are associated with an external referent) and “non-natural meaning” (i.e., the idea that the calls themselves contain semantic content) and so continue to use the term “information” in a rigorous and non-linguistic fashion (see also Wheeler and Fischer 2012). In general, it is the context-specific nature of the calls that is most relevant to understanding how calls function, and not the potential referential content of the calls themselves. Understanding how perceiver responses vary with context thus enables an assessment of how informative calls are, but does not require that calls themselves contain information.

One of the striking features of the debate regarding the referential nature of primate vocalizations is how much rests on the original example of the vervet monkey alarm-calling system. As first noted by Struhsaker (1967), vervet monkeys (*Chlorocebus pygerythrus*) give acoustically distinct alarm calls to each of 3 predator classes. The adaptive responses shown to experimental playbacks of these calls in the absence of the predator (Seyfarth et al. 1980a,b; Cheney and Seyfarth 1992), made them the paradigmatic example of functional reference in non-linguistic organisms (Wheeler and Fischer 2012). Interestingly, given its canonical importance and the extensive research on other taxa that the original study inspired (e.g., Beynon and Rasa 1989; Evans et al. 1993; Zuberbühler 2000),

this work has not been replicated in vervets themselves, although a recent study on the closely related green monkey (*Ch. sabaeus*) has dealt with some of the issues that arise from the original work (Price and Fischer 2013). Besides the intrinsic importance of replication (Kelly 2006), it is also worth re-visiting the vervet case to explore more fully the extent to which contextual factors might influence the response shown to predator calls, as both Scarantino (2010) and Wheeler and Fischer (2012) suggest. It also provides an opportunity to look for evidence that calls might induce certain kinds of affect and hence influence a perceiver’s response.

We have been working on a population of vervet monkeys at Samara Game Reserve in South Africa that matches, in most respects, the historical population in Amboseli, Kenya, where the original alarm call work was done. It is the same species (*C. pygerythrus*), (although new classification now places this in a different sub-species, *Ch. p. pygerythrus* vs. *Ch. p. hilgerti* in Kenya) with a similar population density, ecology, and activity schedule (Pasternak et al. 2013). Our population also experiences levels of predation at least as high as Amboseli although, in the absence of large constricting snakes, only from terrestrial (caracal, *Caracal caracal*; black-backed jackal, *Canis mesomelas*) and aerial (Verreaux’s eagle: *Aquila verreauxii*; giant eagle-owl: *Bubo lacteus*) predators (Pasternak 2011). We have observed predation by, and alarm calls to, all identified predators and the decline in troop size across the study period confirms the importance of predation (see below). Like leopards, caracal, and jackal hunt by stalking and pouncing, while eagles at our site ambush their prey without landing, and then take flight with it (Ducheminsky N, personal observation). As these predatory tactics are similar to those observed at Amboseli, we feel confident that we can discount the possibility that differences in predator behavior will be responsible for any observed differences in the vervets’ responses.

There is, however, an appreciable difference between the 2 populations in relation to group size: riverine groups at Samara are of the order of ~40 animals, which is almost twice the size of those at Amboseli (Pasternak et al. 2013). As a result, group members at Samara also tend to be more widely spaced for most of the day. It is widely accepted that group size is central to predation risk, both because of its consequences for the probability of being attacked (Hamilton 1971) and the likelihood of predator detection through vigilance (Elgar 1989), with larger groups assumed to provide greater protection to their members via both dilution and detection. As Wheeler (2010a,b) has suggested, it seems reasonable to suppose that larger group sizes will result in a greater average distance between callers and perceivers, and hence an increased probability that perceivers will be also be further away from predators, on average, given the range at which predators usually attack. Call distance (which would be perceived as differences in call amplitude) should therefore influence the likelihood that animals will take evasive action. Although Seyfarth et al. (1980b) found that call amplitude had no effect on vervets’ responses at Amboseli, their groups were small and subjects were relatively close to the loudspeaker (~15 m). Given these differences in group size, and hence social context, it is informative to explore whether the Samara vervets display the same responses to predator calls as those at Amboseli, and consider factors that may modulate the relationship between call and response.

Accordingly, we use both observational data on responses to the calls given both to natural predators and those produced during alarm-call playback experiments to test the following predictions:

(i) If alarm calls serve primarily to identify particular predator classes, the first response to a call should be either

context-appropriate predator avoidance behavior or context-appropriate visual scanning.

(ii) If alarm calls show stimulus independence, then there should be no significant difference in the responses produced to natural calls (i.e., when a predator is present) versus experimental calls (i.e., when the predator is absent), whether immediately or in the first 10s following a call.

(iii) Alternatively, in the absence of direct visual evidence of a predator, animals will look more frequently toward the caller as a means to gain further contextual information, that is, they will show a higher tendency to look toward the speaker under experimental conditions where a predator is absent.

(iv) Contextual changes, specifically distance of perceivers from the sound source, will lead to reduced rates of responding as distance from the caller/playback increases.

Finally, we take a first step toward testing the affect-induction model, testing the prediction that:

(v) Both alarm calls and control stimuli should be significantly associated with reflexive startle responses by perceivers due to the sudden onset and plosive quality of the calls (Owren and Rendall 2001).

## METHODS

### Study animals and site

Data were collected between July 2011 and June 2012 from 2 groups of wild vervet monkeys (Riverside Troop, RST, and Riverbend Mob, RBM) at in the Samara Private Game Reserve in the Eastern Cape, South Africa (Pasternak et al. 2013; Henzi et al. 2013). Troop sizes were:  $N_{RST} = 70$  and  $N_{RBM} = 55$  at the beginning of the study period and  $N_{RST} = \sim 60$  and  $N_{RBM} = \sim 35$  at the end of the period. The decline in numbers was a consequence largely of predation (Henzi SP, Barrett L, unpublished data), although pulses of male migration were also a factor. Study animals were fully habituated to the presence of human observers (i.e., they displayed no visible behavioral or vocal response to the observers' presence) and were individually identifiable from natural markings.

### Observational data collection

We collected observational data on a total of 262 days ( $N_{RBM} = 128$ ;  $N_{RST} = 134$ ). Day length varied over the year, given the high latitude of the site (Pasternak et al. 2013) but an average of 10h/day was spent with study animals. Alarm calls were relatively infrequent during this study:  $Mean_{Total} = 0.8$  calls/day ( $Mean_{Land\ predator\ calls} = 0.46/day$ ;  $Mean_{Aerial\ predator\ calls} = 0.25/day$ ;  $Mean_{Snake\ calls} = 0.07/day$ ). As they could not be anticipated, we obtained

observational data on the production and responses to calls by choosing at random a group of visible animals within the group and following it for as long as at least 1 animal, which may or may not have been in the group initially, was visible. When no animals were visible, we moved through the group until we found another animal or animals and followed them. When an alarm call was heard, we used a handheld datalogger (Trimble Juno), equipped with proprietary software to record the first responses of all animals immediately in front of us, their identities and age/sex class, as well as an estimate of their distance in meters from the caller. Observers practiced estimating distance regularly, in order to ensure consistency across different observers and to ensure an acceptable degree of accuracy. Estimates were generally accurate to within 5 m. Responses were categorized as "context-appropriate" or "context-inappropriate" predator avoidance behavior (in accordance with Seyfarth et al.'s (1980b) depictions to ensure comparability across studies: Table 1), as well as "looks toward sound source" and "no observed response." The protocol was also designed to capture predator-specific (vigilance appropriate to the location of the predator, e.g., looking into the sky for aerial predators) and location-specific vigilance (vigilance as determined by the location of the animal, e.g., an animal on the ground may look in response to a terrestrial predator call, but 1 sitting in a tree would look down to the ground).

### Recording of vocalizations

We obtained recordings of predator alarm calls both opportunistically and by presenting the animals with a stuffed caracal, which is the primary predator at the study site, and a model eagle owl. The monkeys' responses to predator mounts resembled closely those of their responses to the actual predators. Mounts were presented to both study troops (caracal:  $N_{RST} = 13$ ,  $N_{RBM} = 9$ ; owl:  $N_{RST} = 8$ ,  $N_{RBM} = 6$ ) and, to reduce the possibility of habituation, repeated presentations were limited to intervals of 14 days or longer. We recorded these calls using a Marantz PMD661 digital recorder connected to a Sennheiser ME67 directional microphone. Complete recordings, chosen for clarity, and recorded within a range of 1.5–6 m, were selected for the playback trials, and edited with the Audacity® Audio editor to produce either single unit (short) or multiple unit (long) calls. Short calls consisted of a single call unit, while long calls comprised, on average, 4 iterations of the call unit (range: 2–7), excised as a subsection of a complete recording. Experimental long calls matched natural calls both in the number of units ( $Mean_{natural} = 4.0$ , range: 2–7) and in their duration ( $Mean_{experimental} = 0.62\text{ s} \pm 0.25$  standard deviation [SD],  $Mean_{natural} = 0.59\text{ s} \pm 0.27$  SD).

**Table 1**

**The classification of evasive behaviors as a function of predator call type and respondent location**

Respondent location	Alarm call type	Respondent behavior					
		Look up	Look down	Run up tree	Run under cover	Run higher up tree	Run down/out of tree
Ground	Aerial predator	Appropriate	NA	Inappropriate	Appropriate	NA	NA
	Terrestrial predator	Inappropriate	NA	Appropriate	Inappropriate	NA	NA
Tree	Aerial predator	Appropriate	Inappropriate	NA	NA	Inappropriate	Appropriate
	Terrestrial predator	Inappropriate	Appropriate	NA	NA	Appropriate	Inappropriate

The designation of responses as appropriate or inappropriate follows Struhsaker (1967) and Seyfarth et al. (1980a,b).

### Experimental procedure and analysis

To ensure comparability with Seyfarth et al.'s (1980a,b) study, we followed their method for experimental playback presentations. Prior to each trial, a Crate TX15 amplifier and speaker was covered by a blanket and transported to the troop's general location where it was hidden behind cover ahead of the anticipated direction of travel by the troop, following the procedure given in (Seyfarth et al. 1980a,b). The digital recorder was used to present the vocalizations, randomized across trials. With the exception of 2 single calls (Tables 2 and 3), each call was presented only once. As is common, in the absence of reference sound pressure level measurements for each of the many calls, we used the independent judgment of other fieldworkers to set appropriate playback volumes (see Seyfarth et al. 1980a,b). Repetitions of each of the 2 calls used in more than 1 playback were broadcast at the same volume. Trial were timed to trade-off the probability that the available animals would veer off in another direction against the distance at which they were from the speaker and likely to detect it. That is, if the approaching monkeys were within 50 m, but no longer moving toward the loudspeaker, or if they were closer than 20 m and appeared to be speeding up, we played the call. The mean distance of subjects at the time of the trial was 32.03 m ( $\pm 15.44$  SD, range: 15–70 m), which is a good match to the mean distance at which subjects heard predator alarm calls during observational data collection (30.1  $\pm$  18.2 m, range: 4–70 m). Given our aim with the experiments was to corroborate our naturalistic observations, we thus did not fully replicate Seyfarth et al. (1980), as their playbacks were conducted at a distance of 15 m from the animals. As we could not find any rationale or justification for the use of this distance reported in their article, we opted against the use of this distance in our study, and conducted playback trials within the range actually experienced by our study animals.

Each troop was presented with land and aerial predator alarm calls recorded from 1 of its members, after ensuring that the original caller was not in the vicinity (see Tables 2 and 3 for details). The bias toward male calls in our sample reflects the fact that, in

**Table 2**  
The provenance of recorded calls used in the playback trials ( $N = 62$ )

Caller age/sex class	Aerial predator calls	Land predator calls
Male	18 + (3)	24 + (4)
Female	1	6
Juvenile	3	3

Two single calls used multiple times are indicated in parentheses. All other calls were used once only.

**Table 3**  
The number of respondents to calls presented during playback trials and calls occurring naturally

Context	Alarm call type	Males	Females	Juveniles	Total
Playback	Aerial	21	14	23	58
	Terrestrial	39	22	35	96
	Total	60	36	58	154
Natural calls	Aerial	28	24	18	70
	Terrestrial	21	25	21	51
	Total	42	42	31	115

our population, females called far less frequently than males and were never observed to produce the first alarm call in response to a predator (Ducheminsky, in preparation). To control for the effects of alarm call length on responses towards alarm calls, we used both long and short alarm calls (see Seyfarth et al. 1980b). We did not present the animals with snake calls or “chutters” (Seyfarth et al. 1980a,b). Although we have evidence that bites by venomous snakes were responsible for fatalities, if not actual predation, snake calls were rarely heard ( $\sim 0.07$ /day) and field observations revealed that monkeys often did not call to snakes that they saw. Our subjective impression of these calls is that they were brief and soft.

We conducted a total of 62 trials (Tables 2 and 3) and used digital video cameras to record responses, with 1–4 people conducting the filming on any 1 trial. We began recording 15 s before the presentation of the call and continued for a minimum of 30 s afterwards. The large inter-individual distances between animals meant that, unlike Seyfarth et al. (1980a,b), we did not wait until a minimum of 5 animals could be filmed and simply obtained what data we could from visible subjects (mean =  $2.42 \pm 2.13$  subjects/trial, range: 1–9). No 2 trials were conducted on the same troop within a 24 h period of the previous playback presentation (Mean<sub>RBM</sub> = 2.8 days, range: 1–7; Mean<sub>RST</sub> = 2.96 days, range: 1–10). Video recordings were subsequently scored independently by 2 people, 1 of whom had not been at the field site, and who did so with reference to the definitions of the relevant behaviors provided by Struhsaker (1967) and Seyfarth et al. (1980a,b).

For the analysis of response times, we added data from the playback of other sounds to serve as an additional control ( $N = 88$  responses from 28 trials). These sounds included human shouts ( $N = 8$  trials), baboon barks ( $N = 5$  trials), antelope barks ( $N = 2$  trials), bird calls ( $N = 6$  trials), and vervet grunts ( $N = 7$  trials). The baboon, antelope, and bird calls were either alarm calls or calls produced when the animals themselves are startled. As such, they should also induce startle responses in perceivers, as they share some of the acoustic features of vervet alarm calls. The same could perhaps be said of human shouts. This means that, in addition to acting as controls, these calls also allow an assessment of the affect-induction hypothesis.

### Data extraction from videotaped responses to experimental calls

Using the 4 categories outlined above, we identified the first response, if any, of each animal to the calls that were played (see Table 1 for descriptions of context-appropriate and inappropriate responses). Again, we used the categories of context-appropriate and context-inappropriate responses as originally used by Seyfarth et al. (1980b) to ensure comparability with their study. The assessment of the outcomes of the original playback experiments at Amboseli was based on the animals' behavior during the 10s following the presentation of the call, with data extraction following a strict protocol (Seyfarth et al. 1980b). Following Seyfarth et al. (1980a,b) and to facilitate more direct comparison, we therefore also scored all identified predator-avoidance behaviors in the 10s that followed the onset of each call. Startles in response to calls were defined as the sudden onset of a full or upper body jerk, with a rapid movement of the head either upwards (if the animal had been looking down) or to one side of the midline.

Interobserver reliability in the scoring of different response categories was high (responses of animals on ground: kappa = 0.98,  $P < 0.001$ ; responses of animals in trees: kappa = 0.92,  $P < 0.001$ ; estimates of visual scanning by subjects: kappa = 0.93,  $P < 0.001$ ).

## Statistical analyses

IBM SPSS statistics software, version 19 (SPSS, Inc., Chicago, IL) generated kappa values for inter-observer reliability in the scoring of the video data. We used the melogit and mixed procedures in Stata 13 (Statacorp. 2013) to run appropriate multilevel generalized linear mixed models on the response data, with logit link functions and binomial errors for the logistic regressions and an identity link function and normal errors for the linear regression.

More specifically, we used mixed logistic regression models to test the probability that an appropriate predator-avoidance response was the first response to alarm calls in both natural and experimental conditions (prediction i). Appropriate response (yes) versus inappropriate response + no predator avoidance combined (no) was entered as the binary dependent variable, troop as an independent control variable, distance from the call as a covariate, and animal identity (nested in troop) as a random effect in order to control for repeated observations of some subjects. We first ran this model on our naturalistic data, and then confirmed these results by running the equivalent model on our experimental data. In addition, to control for the observation of acoustic variability in the calls given to mammalian and avian predators (Struhsaker 1967; Seyfarth et al. 1980b; Ducheminsky N, personal observation), and to test the more conservative prediction—that any form of predator-avoidance behavior will be the first response to natural and experimental alarm calls, rather than no response—we combined appropriate and inappropriate responses into a single category and then re-ran the binary logistic mixed model described above on both natural and experimental data.

To test for a difference between the distribution of responses to natural and experimental calls (predictions ii and iii), we constructed a mixed logistic regression model, in which the context in which the calls were heard (natural or experimental) was the dependent variable, and response type was the independent variable (with this category expanded to include “looks at sound source”). We entered the age/sex class (adult male, adult female, and juvenile) of respondents, troop identity, and distance as general control variables and also included a distance  $\times$  response interaction partly to take into account the volume at which experimental calls were played, but also to investigate the effect that distance had on call responses more generally. Animal identity (nested in troop) was entered as a random effect. Our objective here was to ask whether natural and experimental contexts differed, for which a logistic regression using call context as the binary dependent variable is appropriate, that is, our analysis asks whether the animals’ responses (appropriate, inappropriate, look at speaker) can be used to discriminate between the 2 call contexts (natural vs. experimental).

Where troop is entered into the same model more than once, we did so to allow us to control for the non-independence of individuals, by nesting IDs within troop, and to enable an assessment of the effect of group size by entering troop as an independent control variable. Another source of non-independence is the likelihood that responses are contagious (i.e., the movements of 1 animal triggers movement in others, rather than each responding independently to the call presentation). While a statistical solution to this would be to select a single animal at random from each trial and use its response alone as the datum, this is both wasteful of data and, more importantly, does not control appropriately for contagion. That is, it does not eliminate contagion as an explanation for alarm-call responses more generally: even if a single random individual is used for analysis, the individuals around that animal may

still influence its behavior, hence its response cannot be assumed to be made purely in relation to the call. Contagion, in other words, is an inherent real-world problem. By using all our data, we are able to highlight this as a phenomenon (see Discussion section), rather than generating the impression that there is no possibility of contagion in the data as analyzed. To the extent that there are intrinsic individual response characteristics, we deal with this by including Animal Identity as a random effect.

To compare responses in the 10s following a call, we ran a full factorial mixed logistic regression with response (appropriate/inappropriate) as the dependent variable. We conformed to the Amboseli analytical framework by entering call type (aerial/land predator) and respondent location (ground/tree) as independent variables, with animal identity entered as a random effect.

The inclusion of distance in our models also allowed us to test our prediction that responses of perceivers would be influenced by distance from the caller (prediction iv).

To test prediction v, we used a mixed linear regression analysis with response time (ms) as the dependent variable and troop, distance from loudspeaker and response type (predator avoidance, look at loudspeaker with startle, look at loudspeaker without startle, control response) as independent variables, with animal identity entered as a random factor.

We used log ratio (LR) tests to compare models and, when we do so, we also provide Akaike information criterion (AIC) values, where a lower value suggests a better model fit. Random effects in all models are intercept-only and tests are 2-tailed, with alpha set at 0.05.

## RESULTS

### First responses to natural predator alarm calls

We recorded 136 first responses to naturally occurring alarm calls. Of these, 17 were classified as “context-appropriate” anti-predator responses, 15 as “context-inappropriate” responses, and 65 as “looks toward caller”. We could discern no response at all in 39 cases and did not see any vigilance directed at the predator class indicated by the call (See Table 4 for a full break-down of responses). These data, therefore, indicate that context-appropriate predator-avoidance behavior was not the most common response to calls, nor did animals ever respond with context-appropriate predator-class vigilance.

The results of the binary logistic mixed model analysis confirmed that, in this environment, the absence of context-appropriate predator avoidance was more common than its occurrence (Table 5). This model performed no better than the basal, intercept-only model (AIC = 106.46. LR test:  $\chi^2_2 = 3.14$ ,  $P = 0.21$ ).

When we combined appropriate and inappropriate responses, we found that the probability of some form of active anti-predator response, while still a minority response, was significantly more likely if the alarm caller was closer to the respondent (Table 6). This model performed better than the intercept-only model (AIC = 150.4. LR test:  $\chi^2_2 = 11.03$ ,  $P = 0.004$ ).

### First responses to predator alarm call playback trials

The 62 experimental trials provided 154 individual responses, of which 22 were context-appropriate predator avoidance actions, 18 were context-inappropriate, and 94 were directed at the speaker. We could identify no response at all in 20 cases and did not observe any context-appropriate vigilance directed at the predator class signified

**Table 4**

**The responses of subjects to natural aerial ( $N_{\text{Respondents}} = 70$ ) and terrestrial ( $N_{\text{Respondents}} = 66$ ) predator alarm calls, followed by responses to playbacks of aerial ( $N_{\text{Respondents}} = 58$ ) and terrestrial ( $N_{\text{Respondent}} = 96$ ) predator calls**

Respondent location	Alarm call type	Appropriate		Inappropriate		None		Look to sound source	
		Natural	Expt	Natural	Expt	Natural	Expt	Natural	Expt
Ground	Aerial predator	0	9	8	4	6	3	16	13
	Terrestrial predator	3	3	5	1	4	11	24	34
Tree	Aerial predator	9	0	1	0	12	3	18	26
	Terrestrial predator	5	2	1	4	17	7	19	34

Responses that were neither appropriate nor inappropriate according to the criteria were distinguished by whether the respondent did or did not look toward the sound source.

**Table 5**

**Mixed logistic regression model of the probability that appropriate predator-avoidance responses were the first response to natural alarm calls**

Appropriate/inappropriate	$\beta \pm \text{SE}$	$z$	$P$	95% CI	
Troop (ref: RBM)					
RST	0.736 $\pm$ 0.64	1.15	0.25	-0.52	1.98
Distance	-0.01 $\pm$ 0.01	-1.16	0.25	-0.39	0.01
Constant	-2.81 $\pm$ 1.3	-2.19	0.03	-5.33	-0.3

Troop identity was entered as an independent variable and distance as a covariate. Individual identity was entered as a random factor.  $\beta \pm \text{SE}$  are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios.

AIC = 107.3. Wald  $\chi^2_2 = 2.64$ , NS.

**Table 6**

**Mixed logistic regression model of the probability that any defined predator-avoidance behavior were the first response to natural alarm calls**

Avoidance/none	$\beta \pm \text{SE}$	$z$	$P$	95% CI	
Troop (ref: RBM)					
RST	0.44 $\pm$ 0.42	1.04	0.30	-0.39	1.27
Distance	-0.03 $\pm$ 0.01	-2.82	0.005	-0.05	-0.01
Constant	-1.04 $\pm$ 0.74	-1.41	0.16	-2.5	0.41

Troop identity was entered as an independent variable and distance as a covariate. Individual identity was entered as a random factor.  $\beta \pm \text{SE}$  are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios.

AIC = 143.4. Wald  $\chi^2_2 = 9.32$ ,  $P = 0.009$ .

by the call (Table 4). These data thus confirm the results from the natural calls, demonstrating that context-appropriate predator-avoidance was not the modal response, and that subjects did not respond to calls with predator-appropriate vigilance. We repeated the same analyses that we ran for natural calls and, with the exception of a significant constant, the outcome of the assessment of context-appropriate versus context-inappropriate responses in our experiments was the same as for natural calls, with distance having no effect (Table 7). This model performed no better than the intercept-only model (AIC = 125.54. LR test:  $\chi^2_2 = 4.74$ ,  $P = 0.09$ ).

As for natural calls, when we assessed the likelihood of some form of direct anti-predator response to experimental calls (combining context-appropriate and context-inappropriate responses) (Table 8), we found a significant effect for distance as well as for troop. This model performed significantly better than the intercept-only model (AIC = 169.3. LR test:  $\chi^2_2 = 17.8$ ,  $P = 0.0001$ ).

To investigate whether the latter was a consequence of differences between the troops in their distance to the loudspeaker, we ran a full factorial model. The main effects model (AIC = 155.5) performed as well as the full factorial model (AIC = 155.3. LR test:

$\chi^2_1 = 2.24$ ,  $P = 0.32$ ), indicating that the difference in the responses of the 2 troops was due to the fact that animals in RST were more likely to respond to experimental calls with active evasion of some kind, regardless of distance. Nevertheless, they still did so less than 50% of the time.

### Comparison of first responses to natural and experimental alarm calls

Figure 1 indicates that the modal first response to both natural and experimental calls was to look at the sound source, with the absence of a detectable response as the second most frequent outcome. The full model (AIC = 381.72) performed better than the base model (responses only. AIC = 391.68. LR test:  $\chi^2_7 = 23.9$ ;  $P = 0.0012$ ). Nevertheless, with the exception of troop (RST made a greater contribution to the natural alarm call data set), no variables differed across contexts (Table 9). The same outcome was obtained when the “predator avoidance” response was subdivided into “context-appropriate,” and “context-inappropriate” predator avoidance responses.

**Table 7**

**Mixed logistic regression model of the probability that appropriate predator-avoidance responses were the first response to experimental alarm calls**

Appropriate/inappropriate	$\beta \pm SE$	$z$	$P$	95% CI	
Troop (ref: RBM)					
RST	0.26 ± 0.68	0.39	0.70	-1.06	1.59
Distance	-0.04 ± 0.02	-1.87	0.06	-0.08	0.001
Constant	-1.33 ± 1.24	1.24	0.21	-3.77	1.11

Troop identity was entered as an independent variable and distance as a covariate. Individual identity was entered as a random factor.  $\beta \pm SE$  are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios.

AIC = 124.8. Wald  $\chi^2_2 = 3.75$ , NS.

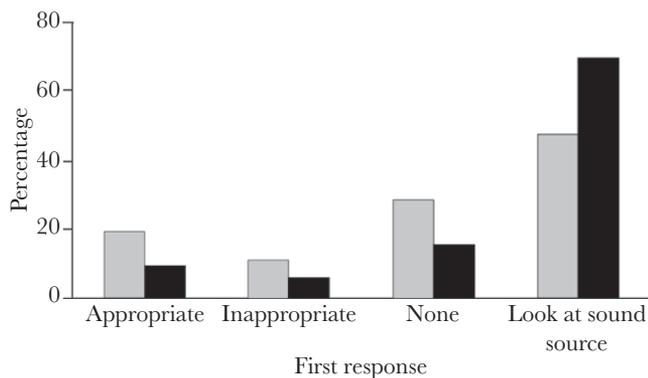
**Table 8**

**Mixed logistic regression model of the probability that any defined predator-avoidance behavior were the first response to experimental alarm calls**

Avoidance/none	$\beta \pm SE$	$z$	$P$	95% CI	
Troop (ref: RBM)					
RST	1.29 ± 0.58	2.21	0.027	0.14	2.43
Distance	-0.06 ± 0.02	-2.91	0.004	-0.1	-0.02
Constant	-1.09 ± 1.04	-1.04	0.30	-3.14	0.96

Troop identity was entered as an independent variable and distance as a covariate. Individual identity was entered as a random factor.  $\beta \pm SE$  are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios.

AIC = 155.54. Wald  $\chi^2_2 = 12.96$ ,  $P = 0.001$ .



**Figure 1**

The relative frequency with which the first response of vervet monkeys to natural (Gray bars.  $N = 136$  animals) or experimentally produced (Black bars.  $N = 154$  animals) alarm calls was (i) predator avoidance, (ii) an absence of any detectable behavior or, (iii) a stare in the direction of the sound source.

### Comparison of responses produced during the 10s following a call

The results of the full factorial mixed logistic regression showed no significant main effect of either call type nor respondent location ( $z_{\text{Call Type}} = -0.22$ ,  $P = 0.83$ ;  $z_{\text{Respondent Location}} = 1.68$ ,  $P = 0.09$ ), nor their interaction ( $z = -0.39$ ,  $P = 0.69$ ). Nor was the model as a whole significant (Wald  $\chi^2_3 = 3.58$ ,  $P = 0.3$ ).

### Startle responses

Examination of the video data from the playback experiments indicated that 76.6% of first responses to alarm calls were accompanied by startle responses. About 88.7% of all “looks toward speaker” responses included a startle as did, definitionally, all predator-avoidance behaviors (see, e.g., Figure 3). Here, it is important to emphasize that the startle and the other actions occurred simultaneously.

By comparison, only 36.3% (32/88) of control calls resulted in animals looking toward the speaker and in no instance was the look accompanied by a startle response. The mixed linear regression analysis revealed that responses to alarm calls that included a startle response were quicker than those without (Table 10. See Figure 2 for overlap in the 95% CIs).

## DISCUSSION

Our observational and experimental results accord with each other, which gives us confidence in the outcomes, but both deviate from prediction in 2 ways. First, the monkeys in our groups never responded to predator alarm calls with context-appropriate, predator-specific vigilance and rarely by initiating active predator avoidance. Second, even when they did do so, there was no support for the prediction that alarm calls associated with each of the 2 primary predator classes the context-appropriate behavior specific to that predator. As such, these results make it difficult to assess the degree of stimulus independence of the calls, given that, in general, there was no overt response to either natural or experimental predator calls. We did, however, find support for the prediction that distance from the caller/speaker would have a significant influence on the likelihood of responding, supporting Wheeler’s (2010a,b) suggestion that animals should be sensitive to call proximity, with greater distance indicating a lower risk of predation to the perceiver. Finally, we found that faster responses to predator calls were significantly associated with the occurrence of startle responses, and that this was specific to vervet alarm calls: the alarm calls of other species were not associated with the production of startle responses.

In some respects, these findings do not deviate as widely from Seyfarth et al.’s (1980 a,b) findings as one might suspect. As Wheeler and Fischer (2012) have recently pointed out, the “textbook account” of vervet alarm-call responding (where animals produce a highly specific, immediate, and unvarying response to each call type) reflects neither Struhsaker’s (1967) initial description, nor the

**Table 9**

**Mixed logistic regression model of the probability that response type (predator-avoidance, look toward call source and no apparent response) differed across call contexts (natural, experimental)**

	$\beta \pm SE$	$z$	$P$	95% CI	
Distance	$-0.024 \pm 0.023$	-1.08	0.28	-0.07	0.02
Age/sex	$-0.28 \pm 0.18$	-1.57	0.12	-0.63	0.07
Troop ID	$1.03 \pm 0.3$	3.36	0.001	0.43	1.63
Distance $\times$ response (ref: predator avoidance)					
None	$0.03 \pm 0.03$	1.05	0.29	-0.02	0.08
Call source	$0.007 \pm 0.025$	0.28	0.78	-0.04	0.05
Response (ref: predator avoidance)					
None	$-0.67 \pm 0.88$	-0.76	0.45	-2.4	1.05
Call source	$-0.96 \pm 0.73$	-1.31	0.19	-2.4	0.47
Constant	$0.11 \pm 0.82$	0.14	0.89	-1.48	1.71

The distance of respondents to the call, age/sex class of respondents (adult male, adult female, and juvenile) and troop identity were included to control for any general influence across call context. The interaction between distance and response type was included to control for the volume at which experimental calls were played and investigate the effect of distance.  $\beta \pm SE$  are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios. Individual identity was entered as a random factor.

AIC = 381.72. Wald  $\chi^2_7 = 25.7$ ,  $P = 0.0005$ .

**Table 10**

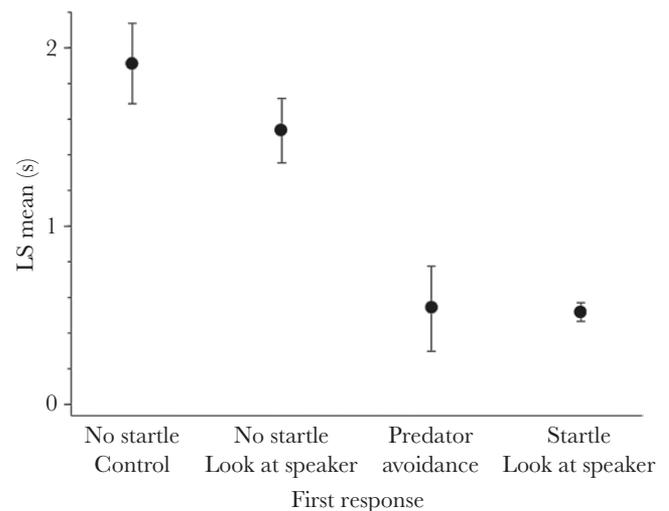
**Mixed linear regression model of the probability that the time of onset of a response to the presentation of an alarm call was a function of troop, distance from the speaker and response type (control, predator-avoidance behavior, look at speaker with startle, look at speaker without startle)**

Time (s)	$\beta \pm SE$	$z$	$P$	95% CI	
Troop (ref: RBM)					
RST	$0.065 \pm 0.067$	0.98	0.33	-0.065	0.2
Response (ref: control)					
Predator avoidance	$-1.02 \pm 0.11$	-9.47	0.0001	-1.59	-1.15
No startle—look at speaker	$-0.02 \pm 0.13$	-2.73	0.89	-0.27	0.24
Startle—look at speaker	$-1.04 \pm 0.08$	-13.12	0.0001	-1.56	-0.92
Distance	$-0.0006 \pm 0.002$	-0.33	0.74	-0.004	0.003
Constant	$1.49 \pm 0.14$	10.47	0.0001	1.23	1.77

$\beta \pm SE$  are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios. Individual identity was entered as a random factor.

Wald  $\chi^2_4 = 339.1$ ,  $P = 0.0001$ .

classic playback experiments themselves, where subjects frequently responded in a context-inappropriate way to the call types with which they were presented (Seyfarth et al. 1980b, Tables VII and VIII). Indeed, the argument for semantic meaning was not derived from the invariance of the animals' responses to the calls; rather, the statistically significant appropriateness of responses was taken to indicate semanticity, much as a word does. The word "fire," for example, always has a referent, but responses to its utterance can be expected to vary according to circumstance. Another way to say this is that the influence of context on the animals' response was implicit in the original work. In this regard, it is important to note that Seyfarth et al. (1980a) observed that their subjects also frequently responded to alarm calls by scanning the environment and looking towards the speaker, "as if searching for additional cues" (p. 802). That is, Seyfarth et al. (1980a) suggested that vervets responded to the potential semantic content of alarm calls in the same kind of context-specific fashion as a person would to the shout of "fire." This being so, a test of their hypothesis does not require that animals produce a single invariant response to each call each time it is heard, rather it suggests that the monkeys' response should be probabilistic and reflect the context of the call; the association is therefore statistical, with a significantly higher probability

**Figure 2**

The onset time (least square mean in seconds  $\pm$  95% confidence interval [CI]) of the first reactions of vervet monkeys to those experimental presentation of alarm and control calls for which a response was detected.

of responding with the appropriate escape response when exposed to a particular predator alarm call. On a descriptive level, then, our findings suggest that greater group size in our population compared to Amboseli results in animals whose context-specific response is to seek more information from their surroundings, rather than produce a reflexive escape response (although, of course, we cannot exclude the possibility that there are other differences in addition to group size that may account for this effect). Unfortunately, we did not have the sample size to conduct a more fine-grained analysis of group-size using the present dataset (e.g., by including group size on the day of the trial) as adding further co-variables would make our models unstable and unlikely to converge. It would be interesting to know the extent to which animals are sensitive to the actual number of other animals present in their vicinity, and how this affects their response.

Why further information-seeking should occur is, however, an open question. One possibility is that, as [Beauchamp and Ruxton \(2007\)](#) show theoretically, larger group size increases the rate of ‘false alarms’ as animals respond mistakenly to innocuous stimuli, which would then make it profitable for animals to seek further information before responding. The greater dispersion of our study groups, and hence the greater average distance at which calls are heard at Samara, may also be a factor here (~30 m in both natural and experimental contexts compared to ~15 m in experimental contexts at Amboseli), given the negative correlation between call distance and active response. As increased inter-individual distances result in fewer close neighbors (as indexed here by the lower number of available subjects in our trials), this may also reduce the likelihood of behavioral contagion (or “response facilitation”: [Hoppitt et al. 2007](#)), which would otherwise be responsible for a more uniform response across animals (i.e., animals respond to the behavioral response of a conspecific rather than to the call itself, see, e.g., [Armstrong 1951](#)). While we very rarely had the clusters of individuals that were common at Amboseli, we did once have a group of 9 animals in an experimental trial, all of which responded to the playback in a synchronized “textbook” fashion ([Figure 3](#)). At the very least, this raises the prospect that proximity increases the likelihood of contagious behavior. Interestingly, a recent study of gray kangaroos (*Macropus giganteus*) makes much the same case for a species that has no alarm calls at all ([Pays et al. 2013](#)). However, if proximity can work in this fashion, it can also create, for the human observer, an impression of independently triggered action driven directly by the call itself. An increase in contagion in smaller groups is a hypothesis that can readily be tested, not only with the significantly smaller groups living in non-riverine habitat at Samara ([Pasternak et al. 2012](#)), but also in other vervet populations, where group sizes are smaller, as well as across different taxa where group size is known to vary systematically.

Another possible factor is that an increase in distance of the perceiver from the caller, as our results indicate, is also likely to reduce the perceived immediacy of any threat, producing responses that are not unnecessarily disruptive to the perceiver ([Wheeler 2010a,b](#)). As a general rule, looking in the direction of the call may actually be the most appropriate response because the caller or others in its vicinity might provide the best indicator of the precise nature and severity of the threat and, therefore, the optimal response.

Group size and dispersion do not, however, explain the fact that, when our animals did take evasive action, their responses were not significantly more likely to be context-appropriate to the predator class in question nor to the animal’s own location in space. Given the similarity of experimental and natural responses, together with



**Figure 3**

A group of 9 vervet monkeys (a) at the moment that the call is presented to them from a distance of 29 m and (b) 300 ms later. Interlacing is visible in (b) because images were extracted from digital video recording.

the fact that the modal response to playbacks at any distance was a reflexive orientation of the head in the direction of the sound source, it is not feasible to argue that the results are a consequence of our experimental procedure. One consideration, however, has to be that we did not use “snake” calls in our trials (and rarely heard them during observational data collection). These calls are soft and acoustically distinctly different, at least in comparison to the calls given to aerial predators ([Owren and Bernacki 1988](#)), and are elicited by snakes in the immediate vicinity of the caller, and it is possible that these may trigger a more stereotyped response in nearby animals. The inclusion of snake calls in the Amboseli study may therefore have contributed more to the overall finding of predator-specific responding, whereas the response to terrestrial and aerial predators may be inherently more variable, and more reliant on surrounding context at the time the call is heard.

Recent work by Price, Fischer and co-workers on West African green monkeys is relevant in this respect ([Price and Fischer 2013](#); [Price et al. 2014](#)). [Price et al. \(2014\)](#) found, for example, that males’ terrestrial predator calls (leopard barks) were also used in male–male competitive displays, suggesting greater variability in the use of this call than originally proposed. In addition, [Price and Fischer \(2013\)](#) found that snake calls were less likely than leopard calls to evoke appropriate responses. This goes against the proposal that snake calls might be responsible for the differences we see between our results and Amboseli, but it should be noted that no direct comparison with our study, nor with [Seyfarth et al. \(1980a,b\)](#), is possible here due to differences in methodology: [Price and Fischer \(2013\)](#) used only female alarm chirps, they could not assess gaze direction due to low visibility; and, most pertinently, used a “prime-probe” approach to test for context-specificity. The real point here, however, is that there is variability in the degree to which particular

predator calls will evoke a context-appropriate response (see also Cäsar et al. 2012). Clearly, further work is needed, and is likely to be valuable and revealing. The absence of snake calls in our playback trials does not, however, detract from the fact that Samara vervets fail to make the predicted discrimination between terrestrial and aerial predator alarm calls.

Given that active behavioral responses to predators were not prevalent in our study, a more comprehensive testing of how context influences vervet monkey responding, including the kinds of affect such calls induce, might pay dividends (see, e.g., Arnold and Zuberbühler 2013; Price and Fischer 2013; Wheeler and Hammerschmidt 2013; Price et al. 2014). While the modal response to alarm calls was simply to look at the call source, it generally shared with active evasion, but not with the response to control calls, its rapid, reflexive nature, and a startle response. This suggests that the increase in arousal generated by the call is an important component of the overall predator response. In fact, if we see active evasion as a particularly strong startle response, provoked by a high amplitude call at close quarters, then their undifferentiated nature is not problematic. On the one hand, this fits with Owren and Rendall's (2001) argument that the concept of information as semantic content may simply be unnecessary: animals do not need to receive information that is "encoded" into a call, "decode" it and then "decide" what to do with the information. Instead, the dimension of interest is signaled directly, and entails a particular response, by virtue of call structure. On the other, the lack of any startle response to control calls argues against this kind of straightforward interpretation, as it suggests that call structure alone is not sufficient to induce a startle. Instead, it suggests that vervet alarm calls are more arousing than those of other species. This could either be because, as per the original "affect conditioning" argument (Owren and Rendall 2001), an actual predator encounter is required for the call to acquire some form of "natural meaning" (Scarantino 2010), and it is this association, and not the call alone, that results in high levels of arousal and startle responses (Owren and Rendall 2001). Alternatively (and this is not necessarily mutually exclusive), vervet alarm calls may be inherently more arousing than the calls of other species, because they are more finely tuned to the vervets' sensory system.

Overall, our results suggest that combining a clear and well-defined notion of "natural meaning" (Scarantino 2010) with elements of an affect induction framework may be a productive route to follow. This would, as Scarantino (2010) suggests, provide the precision argued for by Rendall et al. (2009), by eradicating any sense that calls carry actual informational content, while preserving the idea that useful information can be picked up from the reliable predictive relationship between calls and context. Animal communication can thus consider both information *and* influence, as Scarantino (2010) and Wheeler and Fisher (2012) suggest, without a slide into the inappropriate use of linguistic metaphors.

Regardless of the particular framework in which such investigations are conducted, it seems obvious that much more observational and experimental research on vervets themselves is needed. Beyond a better sense of how different populations and *Chlorocebus* taxa respond to alarm calls in relation to group size and habitat, there remains the unaddressed question, raised by both Struhsaker (1967) and Seyfarth et al. (1980b), of the extent of call variability, both across age/sex classes and as given to particular predator classes. In addition, knowing more about the function of such calls (i.e., do they serve to deter or deflect a predator attack; warn kin; recruit other animals to mob) would help us understand why multiple alarm calls exist in the first

place. It also becomes interesting to ask whether the benefits associated with alarm-calling can be achieved by perceivers if calls cannot be treated as indicative of particular predator type. If we know more, we will then be able to address properly the functional significance of the range of alarm calls available to this species.

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