ALARM CALLS OF VERVET MONKEYS

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Abstract

I used observational data from natural encounters with predators and the controlled presentation of aerial and terrestrial predator alarm calls to assess the hypothesis that these acoustically discernable calls trigger context- and predator-appropriate behaviour in free-ranging vervet monkeys (Chlorocebus pygerythrus). my results, from two study groups in South Africa, show that the modal natural and experimental response was not to initiate escape behaviour, either immediately or in the 10s following an alarm call, but to look at the sound source. When monkeys did take evasive action, which occurred no more frequently than doing nothing at all, contextually- inappropriate behaviour (i.e., behaviour that was not appropriate for evading the specific predator type) was as likely to occur as contextually-appropriate behaviour. I also found that the distance at which calls were heard was negatively correlated with the probability of some form of evasive action. I suggest that the large size of our groups, and the consequently greater mean distance at which natural calls were heard, may explain why our animals displayed low levels of active response and less predator-appropriate evasion or vigilance than expected, given previous work on this species (Seyfarth et al. 1980. Science, 210, 801-803). As the frequency and rapidity with which respondents looked towards the loudspeaker confirmed the general salience of the calls, I 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.

Acknowledgments

Contents

List of Tables

List of Figures

Chapter 1

Introduction

1.1 Selective Forces for Communication

Studies of animal communication have made extensive use of the concept of information, particularly in the realm of vocalizations (see e.g., Hauser (1996); Rendall, Owren, and Ryan (2009); Bradbury and Vehrencamp (2011); Seyfarth and Cheney (2013)). In some instances, such as the early classic studies of primate alarm calling, it was suggested that this information was semantic, and that calls were referential (i.e., they pointed to an external referent, and not merely the animals internal state), with a somewhat arbitrary, word-like structure (Seyfarth, Cheney, & Marler, 1980a, 1980b). An alternative view, put forward around the same time, was that the acoustic structure of calls produced by birds and mammals reflected a more general relationship between the structure of sounds and the motivation underlying their use with, for example, aggressive contexts tending to be associated with harsh, low-frequency sounds (Morton, 1977; Owings & Morton, 1998).

As studies accumulated, particularly on the primates, it became apparent that the structure of calls was not as arbitrary as initially thought, but rather showed evidence of the kinds motivation-structural rules suggested by (Morton, 1977). For review see Wheeler and Fischer (2012). Call production was also shown to be rather inflexible, which further called into question the idea that vocal signals were conventional in the linguistic sense (Wheeler & Fischer, 2012). As a result, there was a shift in terminology: calls were now considered to be functionally referential (Marler, Evans, & Hauser, 1992). That is, they functioned as if they possessed meaning or contained information for perceivers, but with no claims made as to the nature of semantic content, nor any requirement to specify the precise nature of the psychological mechanisms underpinning the perceivers responses. In-

stead, 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 & Fischer, 2012). This notion of functional reference has since been applied widely across both mammalian and avian species (Wheeler & Fischer, 2012).

Some authors have criticized the idea of functional reference, however, on both conceptual and empirical grounds (e.g. Owren and Rendall (2001); Rendall et al. (2009)). Specifically, these authors reject the information concept, arguing that the loose, metaphorical way in which the term is used leads to information being conflated with linguistic notions of meaning (i.e., the idea that calls possess inherent content). As an alternative to functional reference, Owren and Rendall (2001) proposed an affect conditioning or affect induction model that eliminated any reference to language-like metaphors. In this view, which draws on Morton (1977) early work, and Owings and Morton (1998) subsequent assessment-management approach to animal vocal communication, classical conditioning leads animals to associate particular calls with particular contexts, without any requirement for information or semantic meaning to be conveyed by the call itself. Rather, the acoustic structure of the call serves to alert perceivers to the situation, by tapping directly into low-level perceptual, attentional and motivational processes, and animals then learn that these inherently arousing calls predict a particular sequence of events (Owren & 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 information concept in a rigorous and non-linguistic fashion (see also Wheeler and Fischer (2012)). Put simply, 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, 1967a), vervet monkeys (*Chlorocebus pygerythrus*) give acoustically distinct alarm calls to each of three predator classes. The adaptive responses shown to experimental playbacks of these calls in the absence of the predator (Seyfarth et al., 1980a, 1980b; Cheney & Seyfarth, 1992), made them the paradigmatic example of functional reference in non-linguistic organisms (Wheeler & 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, Evans, and Marler (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 & 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 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 perceivers response.

I 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 (*Ch. pygerythrus*), (although new classification now places this in a different sub-species, *Ch. p. pygerythrus*, versus *Ch.p. hilgerti* in Kenya) with a similar population density, ecology and activity schedule (Pasternak et al., 2012). My 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 (Verreauxs eagle: *Aquila verreauxii*; giant eagle-owl: *Bubo lacteus*) predators (Pasternak, 2011). I 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 my site ambush their prey without landing, and then take flight with it (pers. obs.). As these predatory tactics are similar to those observed at Amboseli, I feel confident that I can discount the possibility that differences in predator behaviour will be responsible for any observed differences in the vervets response.

There is, however, an appreciable difference between the two 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., 2012). 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, 2010b) has suggested, it also 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 ~15m. 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, I 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 behaviour 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). (iii) Alternatively, in the absence of direct visual evidence of a predator, animals may look more frequently toward the caller as a means to gain further contextual information (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, I take a first step toward testing the affect-induction model, testing the prediction that (v) Alarm calls should be associated with reflexive startle responses by perceivers due to the sudden onset and plosive quality of the calls (Owren & Rendall, 2001).

Chapter 2
Overview Of The Field

2.1 Selective Forces for Communication

Communication is debatably one of the most challenging constructs to investigate, regardless of the discipline or approach. Defining communication is difficult because there is no universal design or communication system in the animal kingdom; all social animals, in some way, differ in how they communicate with each member of their own species. What is evident in the study of animal communication is that communication requires the interaction of at least two members of the same species. In fact, social groups would not exist without communication between members of each particular group. Thus, for communication to be selected for, group living and interaction with others members must have also been selected for as well.

It often appears that group interaction requires altruistic behaviours that reduces individual fitness for overall group fitness (Trivers, 1971). However, this opposes evolutionary principles that suggest individuals behave to enhance overall fitness for themselves (Dawkins, 2006). Furthermore, group living has many consequences for the individual within the group, such as increased competition for resources and, if not cryptic, increased susceptibility to predation encounters (Hill & Dunbar, 1998). However, social groups are in high abundance today, therefore for many animals, selective forces must have favored individuals to band together and form social groups. To understand animal communication, determining what kind of circumstance(s) would favor group living is the first problem that must be addressed. Predation has been suggested as a primary force that favored group living (Alexander, 1974). It is hypothesized that frequent encounters with predators may have been the big factor that promoted individuals to live cooperative, social lifestyles. Hill

and Lee (1998) analyzed predation risk among 121 different cercopithecoid primate populations and found that predation risk was higher in larger groups relative to smaller groups, suggesting that larger groups are more easily detectable by predators. Why then, would increased risk of being spotted by a predator be favored? This is because predation rate is believed to be lower in larger groups than smaller groups, despite the higher frequency of encounters with predators. To clarify, predation rate is the frequency at which predators successfully attack a group or group member and predation risk is the likelihood of a predator encounter under natural conditions (Hill & Dunbar, 1998). Isbell (1994) found a negative relationship between predation rate and group size in mouse lemurs, suggesting that larger groups indeed helped maintain a lower rate of successful attacks by predators. Hill and Dunbar (1998) have suggested however, that there is not a significant relationship between predation rate and group size in most studies conducted on diurnal species.

Trivers (1971) suggested that once groups form, social behaviour must enhance the original benefits of group living. Group living decreases the odds of a particular individual being predated on over all other members. Living in solidarity means if a predator detects an individual there is no one else the predator will select. Predation risk is lower for any particular individual in a group because other members act as decoys that the predator could select (Hamilton, 1971). Groups also enhance predator vigilance by means of increasing the number of individuals who could locate predators. This is especially effective in animals with evolved alarm calling systems that function to warn other members of nearby predators.

2.2 Historical Theories of Communication in Non-Human Animals

Our understanding of communication systems in all animals, including humans, is not well established and attempting to explain how animals communicate with one another has produced many theories from a variety of disciplines. Early ethological approaches dominated the study of animal behaviour until the middle of the 20th century with Darwins ideas being the catalyst for how ethnologists, such as Lorenz and Tinbergen, approached the study of animal behaviour. Prior to the 1970s it was understood that signals produced by non-human animals evoked a motivational or emotional response in others. Peter Marler was among those to first challenge the traditional dogma as well as assess the structure-function relationship of non-human animal signals. Marlers work led to the discovery of a referential system in a non-human primate population and the birth of the revolutionary informational theories that greatly impacted the future studies of non-human animals.

2.2.1 Early Ethological Theories in Animal Communication

Darwin (1871) suggested that the function of communication systems in animals was to convey information about emotional or motivational states. What intrigued Darwin about social animals was the maladaptive behaviours and expressions that existed despite the considerable consequences that reduced an individuals fitness and chances of survival. The theory of sexual selection, proposed by Darwin (1871) to explain how traits that were exaggerated or showy, such as a bright colours or loud mating calls, were selected for because these traits enhanced reproductive success of the individual. The catch of course being that the exaggerated traits also attract more predators, thus pining sexual selection at

odds with natural selection (Darwin, 1871). Dawkins (2006) describes sexual selection as maintaining individually maladaptive traits in social groups because it provides a mating advantage and those who had a mating advantage, were more fit in terms of reproductive success.

The fathers of ethology, Konrad Lorenz and Nikolaas Tinbergen adopted Darwins thinking that communication was an expression of motivational states. In avian species, Lorenz (1966) studied the material response by mothers towards their young offspring that developed during imprinting stages of development. Tinbergen conducted research on stickleback fish, finding that males were instinctively more aggressive towards wooden models that displayed more red on its underside than a real male fish (Tinbergen, 1952). Tinbergens main premise was that more exaggerated stimuli, or supernormal stimuli, that elicited more of a particular response than the normal stimuli would. Tinbergen (1953) also found that gulls could be made to prefer artificial eggs over their own. Around the same time, Karl von Frisch discovered a unique communication system in honeybees. Von Frisch (1950, 1967) suggested that honeybee expressed information about the location of food sources to one another through different types of dances.

Darwin, Lorenz, Tinbergen and von Finch also acknowledged animal signals as behaviour that benefited other members of the group. In other words, these ethologists took the stance that natural selection for animal signal were observed at the level of the group. Proponents of group selection believed that the function of communication was to improve survival of the group at the expense of individual fitness (Hauser, 1996). For example, alarm calls benefit the group as a whole by alerting the other members of a predator threat, despite increasing ones susceptibly to predation. The problem is explaining why individuals would engage in behaviours that put them at risk. In fact, individuals who dont call go unnoticed by predators and should be more likely to survive. In reality, the fittest individuals are selfish, dont call and increase their chances of survival over those who do (Dawkins,

2006).

In contrast to group selection, gene (or individual) selection suggests that genes, metaphorically, promote their own survival and propagation in future generations over what is best for other group members (Dawkins, 2006). Hamilton (1963, 1964) was the first to suggest that cooperative social behaviour was a means to enhance an individuals inclusive fitness - the direct (mating) or indirect (protecting kin) behaviours that enhancing genetic propagation. Not all social situations are cooperative and individuals within a group interact with each other, even if they are not related. Non-relatives are individuals that stand in the way of ones goals to pass on its genes to subsequent generations. Selection would then favor individuals who could manipulate other individuals within a group. Smith and Price (1973) used game theory to explain the dynamics of all competitive interactions over resources within a population (Smith, 1976, 1977, 1982). Smith and Price described an evolutionary stable strategy occurred in a population when a strategy, that could not bested by an alternative strategy, was adopted by most members of the population. Thus, the best strategy for an individual depends on the nature of competing strategies (Dawkins, 2006). In aggressive conflicts there are two strategies: fight or flee. There are payoffs and costs when choosing a strategy and the population must consist of members that would chose fighting as well as members that would choose fleeing. It is impossible to maintain a system of only fighters or only fleers because a deviant individual who adopts the wrong strategy would be a great advantage in manipulating other members. A stable society must have both individuals who will fight in aggressive situations and those who will flee. Once a population reaches a stable balance of fighters and fleers, the average payoff for fleeing and fighting will be mutual (Smith, 1976, 1977, 1982).

During the 1970s researchers began to move away from the view that signals accurately promoted ones emotions and motivations (Hauser, 1996). During competition, communication functioned to increase ambiguity of emotional states. Zahavi (1975, 1977) intro-

duced the handicap principle - that signals are only honest if they come at a cost to callers. However, these costs would not be as costly in other individuals with less of that particular trait. Zahavis theory accounts for some of the more exaggerated traits that would also attract predation as a side effect, such as loud mating calls or bright colours. Because these traits exist, individuals that display them must be able to cope with, or compensate for, these handicaps. In turn, females will be more attracted to such features because these features indicate high quality partners (Zahavi, 1975, 1977, 1987). An example that demonstrates Zahavis handicap principle is given by the Tungara frog (*Physalaemus pustulosus*). Selection might favor the frogs that advertise best their ability to survive. Typically, Tungara frogs have a whine vocalization but some frogs also display a louder, chuck mating call as well. Females appear to be more attracted the frogs that express wine and chuck calls, perhaps because their louder chucks show an ability to thrive despite a more costly mating call (Ryan, 1990; Ryan & Rand, 1993; Endler & Basolo, 1998).

Perhaps the most promising alternative to the early ethological approaches to communication was outlined by (Dawkins & Krebs, 1978). Adopting the logic of game theory, they suggested that the function of signals during competitive interactions was to manipulate the behaviour of receivers. The manipulation framework was significant to the study of animal behaviour because it provided the first argument that signals were designed to change the behaviour in others, rather than merely inform or deceive others about the signalers intent. At first, Dawkins and Krebs theory was criticized for being signaler-centred and not accounting for communication in highly cooperative species (Van Rhijn & Vodegel, 1980; Hinde, 1981). Krebs and Dawkins responded by acknowledging that receivers would evolve to be good mind readers (Krebs & Dawkins, 1984; Hauser, 1996). In other words there are two parties participating in communication: the signaler, whose intent is to manipulate receivers, and the receiver, whose intent is to try an accurately tell whether or not the signalers expressions are accurate and ignore them if they perceive deception (Krebs &

11

Dawkins, 1984).

Most of the research conducted prior to the 1970s was directed at how animals expressed emotion and motivation states to others or, in the case of manipulation, how signalers could manipulate the emotional states of receivers. Any comparison made to human signals did not extend beyond the level of emotion. No one viewed animal signals as requiring higher-order cognition because non-human animals have less developed neocortical regions of the brain relative to humans (Marler et al., 1992). The honeybee dance in many ways appears to function as if it provides information about the location of a food source is being transmitted from signaler to receiver, in much the same way that humans convey arbitrary messages to one another. However, the structure-function relationships are fundamentally different. Apart from other considerations, there is no homological relationship between the two very different signaling systems (Hauser, 1996).

2.2.2   Structure and Function of Animal Communication

Prior to the 1980s, the predominant view in non-human animal communication was that animal signals primarily reflected changes in arousal or motivation in listeners (Smith, 1977). In contrast to other animals, humans were considered to have the unique ability to do more than express affect. Human language uses complex, arbitrary symbols to refer to objects and events in the world. An example would be how humans can think and communicate about referents, such as food or hunger, outside an immediate context where food is present or they are hungry. The view was that non-human animals could only naturally vocalize indirectly about referents in context-appropriate situation,s via the expression of the communicators internal state (Smith, 1977). In fact, only captive apes and gorillas provided any indication that they could be taught by humans to use signs to communicate (Gardner & Gardner, 1969; Premack, 1970; Rumbaugh, Gill, & von Glasersfeld, 1973; Patterson,

1978; Terrace, 1979) whereas apes in the wild did not do so (LawGoo1968, Fos1972).

Early ethological approaches primarily focused on the functional aspects of non-human animal signals and how they compared to human language. To Darwin (1871), Lorenz (1966), and Tinbergen (1952) animal signals were non-arbitrary expressions of the signalers motivational and emotional states. Peter Marler was the first ethologist to extend this in his analyses of the structure-function relationship of non-human animal signals. Marler (1956) showed that chaffinches used structurally different alarm calls (warning and mobbing calls) in different contexts, which functioned to produce different responses in other chaffinches. The function of warning calls was alert other members of a predator threat that required fleeing action, whereas mobbing calls functioned to localize members and mob the predator threat.

Marlers research on the structure-function relationship in avian species was later redirected to primate vocalizations. Thomas Struhsaker (1967b) first observed that vervet monkeys in Kenya used three distinct alarm calls for three different types of predators. Each alarm call-predator type pairing was associated with a different escape and vigilance response by other members of the group. A sharp tonal bark given to land predators, such as leopards, provoking other vervets to run up a tree and look towards the ground. Low-pitched, staccato grunt calls were given to avian predators and hearing this call would elicit running into cover and scanning upwards for potential avian predators by other group members (Struhsaker, 1967c; Seyfarth et al., 1980a, 1980b). Finally a chutter call, given to snakes and usually produced by females and juveniles, evoked mobbing responses in others, presumably to prevent surprise attacks (Struhsaker, 1967b). Vervet monkeys are uncommonly exposed to a variety of different predator types, virtually leaving vervets with no place to be safe from all predator attacks. Natural forces could select for a communicative design that warned other members, not only of a predator attack, but a specific predator attack. One general alarm call for all predator types wouldnt provide an efficient

13

survival strategy because escaping one predator type could mean being exposed to another predator type (Hauser, 1996). Marler (1967) was the first to suggest that the association between different alarm calls and stereotypical responses towards certain predators appeared to show the semantic features thought to be unique to human languages (Lancaster, 1967; Marshall, 1970).

Approximately 10 years after Struhsakers work (1967b), Marler sent out Robert Seyfarth and Dorothy Cheney to verify experimentally the potential for semantic, or referential, communication. To do so, they augmented the earlier observational work with playback experiments on the same Amobseli vervet population that had been studied by (Struhsaker, 1967b). Seyfarth et al. (1980a, 1980b) hypothesized that, if vervet monkeys displayed the stereotypical responses towards different alarm calls presented to them in the absence of predators, then the vocalizing vervets would be communicating using referential communication. The results of their playback experiments indeed demonstrated that after the presentation of different playback alarm calls, vervet monkeys responded appropriately in the absence of predators Seyfarth et al. (1980a, 1980b). Seyfarth and Cheney concluded that the stereotypical responses were not induced by changes in arousal, but rather by the meaning of the call. For example, when amplitude of the different alarm call types was controlled for, the stereotypical responses remained . Seyfarth et al. concluded that vervet monkeys were using arbitrary signals to communicate the presence of a particular predator in their environment (Seyfarth et al., 1980a, 1980b).

2.3   Informational Theories of Communication

The rudimentary referential alarm calls of the vervet monkeys changed the perception that vocalizations merely reflected changes in affective states. Marler (1977) first suggested that vervet monkey alarm calls represented a rare case of non-affective communication

and the playback experiments conducted by Seyfarth et al. (1980a, 1980b), at the time, confirmed his hypothesis. These findings were revolutionary because it was previously held that humans were the only species capable of semantic communication. Further evidence of the context specificity of the alarm calls came from a follow-up study by Cheney and Seyfarth (1988), that showed that vervet monkeys stop responding to the alarm calls of particular individuals whose recorded calls are were presented frequently in the absence of predators. No responses after false alarm calls by a member of the group suggest that not only is context important for referential communication, but also that memory of prior instances plays a key role in determining whether another member is being honest (Owings & Morton, 1998).

Communication took on a whole new look after Marlers early work with avian and primate animals. Green and Marler (1979) defined communication as the transmission of information from one animal to another. Information is encoded by one individual into a signal and when received by another animal, this information undergoes decoding, while still retaining a specifiable relationship to the encoded information. This definition clearly gives more responsibility to higher cognitive process and moves away from the traditional ideas that communication merely reflects changes in affective states. Animals appear to also convey information about contextual and emotional states. Marlers work, along with that of his colleagues, gave way to informational perspectives that have influenced much of the research conducted in animal communication over the past 30 years.

Seyfarth et al. (1980a, 1980b) adopted the informational hypothesis when they concluding that vervet monkey alarm calls were evidence that a form of referential communication could exist in non-human animals. They importantly acknowledge that these alarm calls are not exactly like human words; a leopard alarm call doesnt mean leopard in the same sense that humans use the word leopard. Instead, early informational theories characterizes animal signaling as a process in which the signaler generates and encodes information about a

particular stimulus in their environment and conveys this information to a receiver(s) who, in turn, relies on evolved neural and perceptual processes to decode and recover this information (Green & Marler, 1979). Early informational approaches have been criticized for failing to define constructs like information and encoding. (Owren & Rendall, 2001; Rendall et al., 2009; Owren, Rendall, & Ryan, 2010), since the suggestion that calls carried encoded information put biological constructs secondary to linguistic constructs. This is problematic because what it is exactly that is encoded as information is left unknown. Constructs like reference or semanticity are, for Owren and Rendall (2001), merely metaphors referring to encoded information.

Owren and Rendall (2001) pointed out that early informational approaches were at odds with the evolutionary principles like gene selection and the selfish gene principle. For example, alarm calls produced by signalers were believed to function to enhance the survival of other group members. As stated earlier, however, it would be the individuals who refrain from calling that hold the advantage over callers because they would not be located as easily by predators (Dawkins, 2006). Kin selection and altruism are not highlighted as principles of early informational theories, thus leaving no explanation for why apparently altruistic alarm calls that contain information about a potential predator threat exist Owren and Rendall (2001). Although Seyfarth et al. (1980a) acknowledge that acoustic features are likely to play a partial role in eliciting responses towards different predators (i.e. without arousal, there would be no panic responses at all to any predator) the majority of the effect is a consequence of higher cognitive processing. In other words, informational approaches do not describe the relationship of the acoustical properties of alarm calls and their function. Suggesting that there is no relationship between the morphology of different alarm calls and the stereotypical responses is taking a giant step away from the processes that govern the majority of animal expressions. It is not impossible think that different alarm calls could simply be conditioned to different responses, much like how many animal vocalizations are

16

developed over generations.

Informational approaches are also problematic in that they turn evolution on its head (Owren & Rendall, 2001; Rendall et al., 2009; Owren et al., 2010). One important principle of evolution is that it works through the modification of existing characteristics (Hall, 2003). For example, the evolution of bipedalism is best approached by examining the relationship of structural and functional characteristics of bipedal locomotion and ancestral quadrupedal locomotion in common ancestors. Instead, informational perspectives examine the language-like properties animal signals without providing morphological and neuroanatomical evidence in any common ancestors (Owren et al., 2010). Unfortunately, the mechanisms involved in human language and all other non-human animal communication are distinct, whereas parallels to other communicative designs in common ancestors would be more sensible (Owren et al., 2010). For example there are no shared mechanisms in honeybee dancing and human language as they share no common ancestors (Von Frisch, 1950, 1967). As humans share many ancestral characteristics to primates, it is quite enticing to look for similarities in human and non-human primate communication. Both humans and many primate species are very social creatures and have higher brain sizes than should be expected given their body size (Passingham, 1981). However the brain structures of humans and other primates are still very different. Human language goes beyond stimulating the subcortical, emotional regions of the brain. Human language activates the prefrontal cortex regions of the brain along with the subcortical regions (Lieberman, 2002). Studies have shown that when non-human primates communicate, mostly only the subcortical regions of the brain are stimulated, indicating that animal communication is not really human-like (Radick, 2005).

Referential communication had a great impact on animal communication in the years following the Amboseli playback study. However, it had becoming increasing evident that animal signals were still strikingly different from human words. Informational theories

decided to modify the definition of referential communication rather than abandon it all together. Functional referentiality was adopted as a term in order to distinguish the features of non-human communication from those of human language (Hauser, 1996). Functionally referential signals are context-specific signals, which elicit the same response as the referent for which the signal stands, even in its absence (Evans, 1997). The purpose of adopting functional referentiality was to abandon the idea of intentional signaling via the encoding of information while maintaining the idea that signals had independent meaning (Cheney & Seyfarth, 1996). However, informationalists still hold that functional referential signals require higher cognitive processes and are closer to human language than any other form of communication in non-human animals (Marler et al., 1992).

The informational perspectives attribute higher cognitive processes, though not always specified, as an explanation for animal signals. Informational perspectives, as outlined above, have come under scrutiny, and opposing perspectives have gained as much attention over the last two decades as the informational perspectives. (Marler, 1977) began to move away from the idea that animal signals only elicited affective responses in receivers. Around the same time that Seyfarth et al. (1980a, 1980b) were uncovering the referential alarm calls of vervet monkeys, (Dawkins & Krebs, 1978) were arguing that signals functioned to manipulate receivers, with the receivers objective being to resist (Krebs & Dawkins, 1984). The two perspectives carry different expectations. Referential communication requires that signals benefit the receiver along with the signaler. A battle between manipulative signalers and resisting receivers, on the other hand, is the selfish behaviour that is expected from two animals with divergent fitness interests (Owren et al., 2010). Receivers learning to ignore manipulative signals would force signalers to become honest, at least some of the time, creating an environment with a wide array of communicative interactions.

2.4 Influence over information: The affect-induction approach

Many researchers believe that terms like information and encoded information cloud our understanding of animal communication. Though there have been many criticisms of the informational theories, textbooks still refer to vervet alarm calls as being like human words as if the definition of communication proposed by Green and Marler (1979), is still accurate today. Metaphorical comparisons of human words to animal vocalizations that appear representational do not highlight any underlying morphological or physiological mechanisms involved in producing and responding to vocalizations. Informational definitions are susceptible to conflating information with meaning, in turn producing indefinable, non-measurable constructs. Since 1980, researchers have been propelled towards analyzing higher cognitive processes in animals with semantic like signals rather than focus on the acoustic characteristics of vocalizations or the sensory systems at play when vocalizations are produced and heard (Owren & Rendall, 2001; Rendall et al., 2009; Owren et al., 2010).

Owren and Rendall have proposed that the current definition of communication needs to move away from loosely defined terms such as information, encoding, decoding and representation. They suggest that communication is better described as specialized, species-typical morphology or behaviour [selected] to influence the current or future behaviour of another individual (Owren et al., 2010). A definition based on influence instead of information appropriately incorporates all communicative circumstances, whether it be in cooperative situations, such a courtship calls or predator calls, or competitive circumstances, such as aggressive encounters. This affect-induction (Owren & Rendall, 2001) approach is very similar to the definition proposed by (Krebs & Dawkins, 1984). Instead of signalers manipulating receivers, the affect-induction account proposes that signalers influence a response in receivers (Owren & Rendall, 2001; Rendall et al., 2009; Owren et al., 2010).

A major advantage of the affect-induction approach is that affect and emotional responses abide by the principles of evolution. Affect-induction is explicitly signaler-centered whereas the informational approaches are largely assuming social behaviour resulted from cooperative evolution where signalers shared encoded information with others (Owren & Rendall, 2001). When signalers are influencing the behaviours of receivers, they always benefit. Receivers can benefit, but not in all circumstances. In other words, the affect-induction proponents would state that vocalizations do not function to benefit receivers. In fact, (Owren et al., 2010) suggest that vocalizations that benefit receivers are likely to be secondary consequences of other evolved perceptual mechanisms. For example alarm calls may have evolved as a secondary behaviour following the pairing of stereotyped escape responses with particular predators. If the limbic system produces different states of arousal to different predators because it provided a better strategy to escape that particular predator, then it is not impossible that different sounds would also become paired with these particular predator-response associations. In fact, affective accounts do not attribute higher cognitive mechanisms that would be required for referential communication and suggest, instead, that different signal designs influencing affective responses in other individuals become paired via conditioning. To make referential-like animal signals more affect-based puts these signals on par with other evolved conditioned behaviours in animals. Instead of introducing higher cognitive mechanisms into animal communication, signals can now be viewed like most other animal behaviours that are governed by sensory and emotional processes.

When you analyze the acoustic structure and subsequent responses of mating calls, it is evident that these calls need not contain encoded information about a particular mates fitness that must be decoded by females. For example, the chuck mating call of the Tungara frog may be favored because whine calls were insufficiently audible against background noise (Ryan, 1990). Male Tungara frogs are the only species of frog in its clade to produce

the chuck call and it is extremely effective in attracting mates, including those from other frog species. It has been suggested that two organs of the Tungara frogs ear are sensitive to different calls, a trait characteristic of many anuran species (Gerhardt & Schwartz, 2001). The amphibian papilla is sensitive to whines and the basilar papilla is more sensitive to chucks, a sensory design that males can be selected to exploit in females (Ryan & Rand, 2003). This is further evidence that signalers clearly benefit. Although females appear to benefit this may be a derived effect of the evolution of the anuran sensory systems. Receivers can become habituated to vocalizations and therefore learn to stop responding to calls that induce less of a physiological response. Even vocalizations that appear to be arbitrary at first, such as the vervet monkey alarm calls, are clearly anything but. To evoke any kind of response in in listeners, there must be an affective response that precedes an escape response.

2.5   History of playback experiments

Prior to Seyfarth and Cheneys initial playback experiment on vervet monkeys there was only a small sample of playback experiments conducted on other animals. Garner (1891, 1892) is best known for being the first to use a playback experiment while studying simian vocalizations and their relationship to human words. A notable playback program that preceded the 1980s was Huxley and Koch (1938) work in which they recorded and played back the vocalizations of mandrill, mangabey, and baboons and assessed how they responded. At much the same time Carpenter (1941) conducted playbacks on gibbons in Thailand. At the same time, it was clear that playbacks were not being used as a primary tool for studying animal communication and the meaning of animal signals (Radick, 2005).

Vervet monkeys not only became the public face of language-like calls and referential communication but also opened the door for the use of playback experiments to analyze the

meaning of animal vocalizations. With the technology for the time, Seyfarth and Cheney experiment demonstrated that playback studies could be conducted in an animals natural environments and provide a useful means to assess the effects of animal vocalizations outside appropriate contexts (i.e. alarm calls in the absence of a predator). They did more than just assess vervet monkey alarm call for the potential of referential communication. Using playbacks, Cheney and Seyfarth (1982) showed that different grunts produced by vervet monkeys evoked different responses that were dependent on the acoustic properties of each grunt. Cheney and Seyfarth reported that the different responses to different grunts were more subtle than the different responses following alarm calls, but still significant enough for them to suggest that they pointed to rudimentary referential communication (Cheney & Seyfarth, 1982). Cheney and Seyfarth (1985) also used playback studies to verify Dawkins and Krebs hypothesis that animals signals functioned to manipulate others (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984). Following playbacks to alarm calls, lower ranking vervets appeared to have withheld alarm calls when in the presence of high-ranking individuals more often than high-ranking individuals withheld calls after spotting predators. This hypothesis was more difficult to confirm in their early experiments, even on captive groups. In another study, Cheney and Seyfarth (1988) assessed signal habituation and whether vervets learned to ignore intergroup chutters and alarm calls from vervets that consistently vocalized at inappropriate times. This study was also important because it contrasted acoustically different vocalizations, their apparent functions and whether habituation occurred across one call or all calls from a particular individual. As with previous research on vervet vocalizations, they provided evidence that the information was understood at the semantic level when vervets learned that certain contexts, alarm calls do not always provide reliable information, such as when a vervet constantly cries wolf (Cheney & Seyfarth, 1982; Owings & Morton, 1998).

Work on squirrels that followed the Amboseli playback experiment, found mixed evi-

dence for referential communication. Belding squirrels (*Spermophilus beldingi*) (Robinson, 1980, 1981) and California ground squirrels (*Spermophilus beecheyi*) (Owings & Hennessy, 1984) both responded to flying raptors with a high sense of urgency relative to the low urgency responses elicited by terrestrial predators. Owings, Hennessy, Leger, and Gladney (1986) reported that, in terms of responding to terrestrial and rattlesnake predators, the function of alarm calls was to warn vulnerable offspring. For mammalian predators, it appeared that only alarm calls that were non-repetitive calls functioned as warning alarm calls. Consequently, Greene and Meagher (1998) reported that red squirrels have acoustically distinct predator alarm calls. Seet calls were produced towards aerial predators and bark calls were produced mostly towards terrestrial predators. However these studies didnt conduct playback experiments and therefore did not establish whether calls were truly referential or urgency based. Playback experiments on Colombian ground squirrels (*Urocitellus columbianus*) have provided evidence that recorded vocalizations are context specific. Harris, Murie, and Duncan (1983) concluded from playbacks that hollow chirps function to elicit attention in others, but not in an alarm circumstance, while shrill chirps function as predator alarm calls.

The emergence of playback experiments on other primate species became apparent in the 1990s. Macedonia (1990) conducted a similar playback study on ring-tailed (*Lemur catta*) and ruffed lemurs (*Vavecia varieata*), both of which are known for having distinct terrestrial and aerial alarm calls. His results indicated that ring-tailed lemurs could distinguish between terrestrial and aerial predators. Ringtailed lemurs looked up and locomoted bipedally when hearing an aerial alarm call, and ran up trees before looking down after terrestrial alarm calls were emitted, even in the absence of the predators. Thus, the ring-tailed lemurs did appear to respond referentially towards aerial and terrestrial alarm calls. On the other hand, ruffed lemurs did not do so. Their most common response to either alarm call was to look in the direction of the speaker, rather than scan for a particular predator and

responses that did occur to alarm calls were based on level of perceived threat, rather than type of predator (Macedonia, 1990).

Along with his colleagues, influential primatologist Klaus Zuberbhler and colleagues have studied primate communication in Diana and Campbells monkeys. Males of both species respond to alarm calls of aerial and terrestrial predators stereotypically. Zuberbühler, Noë, and Seyfarth (1997) discovered that Diana monkeys (*Cercopithecus diana*) produce distinct calls towards leopard and aerial predators. After conducting playback experiments on male Diana monkeys, the apparent function of the alarm calls appeared to be to warn others of a particular predator threat and communicate the detection of a predator. Female and male Campbells monkeys (*Cercopithecus campbelli*) produce vocalizations in different contexts from each other (Ouattara, Lemasson, & Zuberbühler, 2009b, 2009a). Ouattara, Zuberbühler, N'goran, Gombert, and Lemasson (2009) compared predator specific alarm calls of captive female to wild female Campbells monkeys and found that only wild monkeys produced predator specific alarm calls. Their playback experiment was not typical of other playbacks in that they played recordings of leopard growls and eagle shrieks, along with presenting leopard, eagle and python mounts in order to compare females responses to all five predator situations. Females produced three types of calls (hoks, wak-oos and RRA calls) in predator situations. Furthermore, there were a variety of RRA calls that were distinguishable and context-specific. For example, (Ouattara, Lemasson, & Zuberbühler, 2009b) observed that RRA4 calls are primarily given towards leopard and snake predators and RRA3 calls being given, along with hoks and wak-oos, to crowned eagles. Though the authors believe these calls could be referential, a playback experiment that measures the different responses towards calls needs to be done in the absence of the particular context. Finally, urgency models were supported by the fact that females respond with more urgency towards visual encounters with predators, rather than audible playbacks of aerial predators.

There have been plenty of playback experiments conducted over the last 30 years, many of which were aimed as assessing the potential for referential communication in non-human animals. Playback experiments conducted on suricates (*Suricata suricatta*) by Manser, Bell, and Fletcher (2001) found that they responded differently to the alarm calls of aerial predators than they did to land predator alarm calls. Suricates also responded differently based on level of urgency in the alarm calls. Manser concluded that suricates were retrieving information about the type of predator and urgency of the call from the different alarm calls from the alarm calls. As Mansers experiment shows, it is clear that it is not possible obtain all the answers about animals communication based solely on playback experiments, but they are very useful tools for assessing animal behaviour, nonetheless. With technology becoming increasingly advanced, tools like playbacks will surely continue enhance our understanding of what is evidently one of the most convoluted areas of study. Remarkably, given its canonical importance and the extensive research on other taxa that the Seyfarth et al. (1980a, 1980b) study spawned (Beynon & Rasa, 1989; Evans et al., 1993; Zuberbühler, 2000), their work on vervets has not been replicated; although a recent study on the closely-related green monkey (*Chlorocebus sabaeus*) has dealt with some of the issues that arise from the original work (Price & Fischer, 2013).

Chapter 3

Methods

3.1 Study Animals and Site

Data were collected between July 2011 and June 2012 from two 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. 2012; Henzi et al. 2013). Troop sizes were: $N_{RST} \cong 70$ and $N_{RBM} \cong 55$ at the beginning of the study period and $N_{RST} \cong 60$ and $N_{RBM} \cong 35$ at the end of the period. The decline in numbers was a consequence largely of predation (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 behavioural or vocal response to the observers presence) and were individually identifiable from natural markings.

3.2 Observational data collection

I 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. 2012) but an average of 10hrs/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, I 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 one animal, which may or may not have been in the group initially, was visible. When no animals were visible, I moved through the group until I found another animal or animals and followed them.

When an alarm call was heard, I 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 metres 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 5m. Responses were categorised as context-appropriate or context-inappropriate predator avoidance behaviour (in accordance with (Seyfarth et al., 1980b) depictions: Table 3.1), as well as looks towards 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 up in response to a terrestrial predator call, but one sitting in a tree would look down to the ground).

3.3   Recording of vocalizations

I 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. I 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 1.5-6m, 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, four 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$_{experimental}$ = 0.62ms+/-0.25SD, Mean$_{natural}$ = 0.59ms +/-0.27SD).

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

Table 3.1: The frequency with which vervet monkeys responded with either appropriate (N = 22) or inappropriate (N = 18) predator-avoidance behaviour in the 10s following the experimental presentation of an alarm call. The number of animals that did not produce predator-avoidance behaviour (N = 114) is also indicated.

3.4 Experimental procedure and analysis

To ensure comparability with Seyfarth et al. (1980a, 1980b) study, I 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 troops 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, 1980b). The digital recorder was used to present the vocalisations, randomised across trials. With the exception of two single calls (Table 3.2), each call was presented only once. As is common, in the absence of reference sound pressure level measurements for each of the many calls, I used the independent judgment of other fieldworkers to set appropriate playback volumes (see Seyfarth et al. (1980a, 1980b)). Repetitions of each of the two calls used in more than one playback were

broadcast at the same volume. The trial was 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 50m, but no longer moving towards the loudspeaker, or if they were closer than 20m and appeared to be speeding up, I played the call. The mean distance of subjects at the time of the trial was 32.03m (+/-15.44SD. Range: 15m-70m), which is a good match to the mean distance at which subjects heard predator alarm calls during observational data collection (30.1m +/-18.2m. Range: 4m-70m). Given that my aim with the experiments was to corroborate my naturalistic observations, I thus did not fully replicate Seyfarth et al. (1980a, 1980b), as their playbacks were conducted at a distance of 15m from the animals. As I could not find any rationale or justification for the use of this distance reported in their paper, I opted against the use of this distance in my study, and conducted playback trials within the range actually experienced by my animals.

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

Table 3.2: Number of times an individuals playback was used (number of alarm calls that were re-used in a second playback.)

Each troop was presented with land and aerial predator alarm calls recorded from one of its members, after ensuring that the original caller was not in the vicinity, and, with the exception of one aerial call and one land call that were used on more than one occasion, each call was presented only once (see Table 3.2 for details). The bias towards male calls reflects the fact that, in our population, females called far less frequently than males and were never observed to produce the first alarm call in response to a predator. To control for the effects of alarm call length on responses towards alarm calls, I used both long and short

		Males	Females	Juveniles	Total
Playbacks					
	Aerial	21	14	23	58
	Land	39	22	35	96
	Total	60	36	58	147
Natural					
	Aerial	28	24	18	70
	Land	21	25	20	66
	Total	49	49	38	136

Table 3.3: Sex/Age of respondents to calls during playback trials and calls occurring naturally.

alarm calls (see Seyfarth et al. (1980b)). I did not present the animals with snake calls or chutters (Seyfarth et al., 1980a, 1980b). Although I 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. My subjective impression of these calls is that they were brief and soft.

I conducted a total of 62 trials (Table 3.3) and used digital video cameras to record responses, with one to four people conducting the filming on any one trial. I began recording 15 sec before the presentation of the call and continued for a minimum of 30sec afterwards. The large inter-individual distances between animals meant that, unlike Seyfarth et al. (1980a, 1980b), I did not wait until a minimum of five animals could be filmed and simply obtained what data I could from visible subjects (mean = 2.42 +/-2.13 subjects/trial. Range: 1-9). No two trials were conducted on the same troop within a 24hr period of the previous playback presentation (Mean$_{RBM}$ = 2.8 days, Range: 1-7; Mean$_{RST}$ = 2.96 days, Range: 1-10). Video recordings were subsequently scored independently by two people, one of whom had not been at the field site, and who did so with reference to the definitions of the relevant behaviours provided by (Struhsaker, 1967a) and Seyfarth et al. (1980a, 1980b).

For the analysis of response times, I 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.

3.5   Data extraction from videotaped responses to experimental calls

Using the four categories outlined above, I identified the first response, if any, of each animal to the calls that were played (see Table 3.1 for descriptions of context-appropriate and inappropriate responses). The assessment of the outcomes of the original playback experiments at Amboseli was based on the animals behaviour 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, 1980b) and to facilitate more direct comparison, I therefore also scored all identified predator-avoidance behaviours in the 10s that followed the onset of each call. Startles in response to calls were defined as a sudden onset 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.

Inter-observer 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).

3.6   Statistical Analyses

IBM SPSS statistics software, version 19 (SPSS Inc., Chicago, IL, U.S.A.) generated kappa values for inter-observer reliability in the scoring of the video data. I used the melogit and mixed procedures in Stata 13 to run appropriate multilevel generalised 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. In each, animal identity (nested in Troop) was entered as a random effect in order to control for repeated observations of some subjects. I used the log ratio (LR) test to compare models and, when I do so, I also provide Akaike information criterion (AIC) values, where a lower value suggests a better model fit. All tests are two-tailed, with alpha set at 0.05.

Chapter 4

Results

4.1 First responses to natural predator alarm calls

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

Table 4.1: The responses of subjects to natural aerial ($N_{Respondents}$ = 70) and land ($N_{Respondents}$ = 66) predator alarm calls, followed by responses to playbacks of aerial ($N_{Respondents}$ = 58) and land ($N_{Respondent}$ = 96) predator calls. Responses that were neither appropriate nor inappropriate according to the criteria were distinguished by whether the respondent did or did not look towards the sound source.

I 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 towards caller. I 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 4.1 for a full break-down of responses). These data, therefore, indicate the predicted context-appropriate predator-avoidance response was not the most common response to calls, nor did animals ever respond with context-appropriate predator-class vigilance. As some animals contributed more than one datum, I assessed the extent of context-appropriate anti-predator behaviour statistically with a binary logistic mixed model (appropriate response versus inappropriate + no predator avoidance) with Troop as an independent control variable, Distance from the call as a covariate, and Animal Identity (nested in Troop)

as a random effect. The results confirm that, in this environment, the absence of context-appropriate predator avoidance was more common than its occurrence (Table 4.2A). This model performed no better than the basal, intercept-only model (AIC = 106.46. LR test: $\chi^2_{22} = 3.14$, P = 0.21).

To control for the observation that there is some acoustic variability in the calls given to mammalian and avian predators (Struhsaker 1967; Seyfarth et al. 1980b; pers. obs.), and to test the more conservative predictionthat calls will elicit at least some form of predator-avoidance behaviour I combined appropriate and inappropriate responses (N=32) and re-ran the logistic model (Table 4.2B). Here, I 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. This model performed better than the intercept-only model (AIC = 150.4. LR test: $\chi^2_{22} = 11.03$, P = 0.004).

4.2   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. I could identify no response at all in 20 cases and did not observe any context-appropriate vigilance directed at the predator class signified by the call (Table 4.1) 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. I repeated the same analyses that I ran for first responses to natural calls and, with the exception of a significant constant, the outcome of the assessment of context-appropriate versus context-inappropriate responses in my experiments was the same as for natural calls, with distance having no effect (Table 4.3A). This model performed no better than the intercept-only model (AIC = 125.54. LR

test: $\chi^2_{22} = 4.74$, P = 0.09)

A.

Appropriate/ Inappropriate	β+/-SE	z	P	95% CI	
Troop (ref: RBM)					
RST	0.736+/-0.64	1.15	0.25	-0.52	1.98
Distance	-0.01+/-0.01	-1.16	0.25	-0.39	0.01
Constant	-2.81+/-1.3	-2.19	0.03	-5.33	-0.3

AIC = 107.3. Wald X^2_2=2.64, NS

B.

Avoidance/ None	β+/-SE	z	P	95% CI	
Troop (ref: RBM)					
RST	0.44+/-0.42	1.04	0.3	-0.39	1.27
Distance	-0.03+/-0.01	-2.82	0.005	-0.05	-0.01
Constant	-1.04+/-0.74	-1.41	0.16	-2.5	0.41

AIC = 143.4. Wald X^2_2=9.32, P=0.009

Table 4.2: Mixed logistic regression model of (A) the probability that appropriate predator-avoidance responses and (B) the probability that any defined predator-avoidance behaviour were the first response to natural alarm calls. Troop identity was entered as an independent variable and Distance as a covariate. Individual identity was entered as a random factor. β+/-SE are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios.

As for natural calls, when I assessed the likelihood of some form of direct anti-predator response to experimental calls (combining context-appropriate and context-inappropriate responses) (Table 4.3B), I 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: $\chi^2_{22} = 17.8$, P = 0.0001).

To investigate whether the latter was a consequence of differences between the troops in their distance to the loudspeaker, I 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: $\chi^2_{21} = 2.24$, P = 0.32), indicating that the difference in the responses of the two troops was due to

35

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.

A.

Appropriate/ Inappropriate	β+/-SE	z	P	95% CI	
Troop (ref: RBM)					
RST	0.26+/-0.68	0.39	0.7	-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

AIC = 124.8. Wald X^2_2=3.75, NS

B.

Avoidance/ None	β+/-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	0.3	-3.14	0.96

AIC = 155.54. Wald X^2_2=12.96, P=0.001

Table 4.3: Mixed logistic regression model of (A) the probability that appropriate predator-avoidance responses and (B) the probability that any defined predator-avoidance behaviour were the first response to experimental alarm calls. Troop identity was entered as an independent variable and Distance as a covariate. Individual identity was entered as a random factor. β+/-SE are coefficients and their associated SEs in logits. 95% confidence intervals (CI) are derived from transformed odds-ratios.

4.3 Comparison of first responses to natural and experimental alarm calls

Figure 4.1 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. I tested the prediction that responses to natural and experimental calls would not differ with a Response category that was broadened to include looks at sound source. I entered the Age/Sex class (Adult Male, Adult Female, Juvenile) of respondents, Troop Identity and Distance as general control variables and Distance*Response 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. The final model (AIC: 381.72) performed better than the base model (Responses only. AIC: 391.68. LR test: $\chi^2_{27} = 23.9$; P = 0.0012). Nevertheless, with the exception of Troop ID (RST made a greater contribution to the natural alarm call data set), no variables differed across contexts (Table 4.4). The same outcome was obtained when the predator avoidance response was subdivided into context-appropriate and context-inappropriate predator avoidance responses.

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

I ran a full factorial mixed logistic regression of the Samara data with Response (Appropriate/Inappropriate) as the dependent variable. I 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. Neither main effect ($z_{Call Type} = -0.22$, P = 0.83; $z_{Respondent Location} = 1.68$, P = 0.09), nor their interaction ($z = -0.39$, P = 0.69), was significant, nor was the model as a whole (Wald $\chi^2_{23} = 3.58$, P = 0.3).
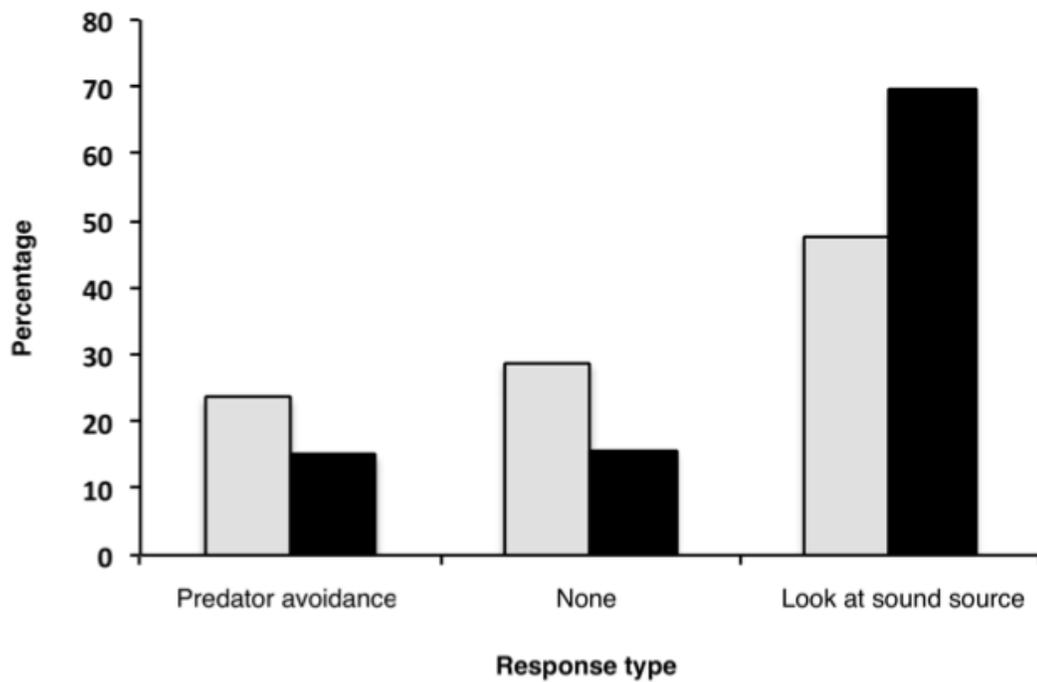
Figure 4.1: The relative frequency with which the first response of vervet monkeys to natural (Grey bars. N = 136 animals) or experimentally-produced (Black bars. N = 154 animals) alarm calls was i. predator avoidance, ii. an absence of any detectable behaviour or, iii. a stare in the direction of the sound source.

4.5   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. 88.7% of all looks toward speaker responses included a startle as did, definitionally, all predator-avoidance behaviours (see, for example, Figure 4.1). Here, it is important to emphasise that the startle and the other actions occurred simultaneously. By comparison, only 36.3% (32/88) of control calls resulted in animals looking towards the speaker and in no instance was the look accompanied by a startle response. 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, revealed that responses to alarm calls that included a startle response were quicker than those without. (Table 4.5. See Figure 4.2 for overlap in the 95% CI).

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

Table 4.4: Mixed logistic regression model of the probability that Response type (predator-avoidance, look towards call source and no apparent response) differed across Call contexts (natural, experimental). The Distance of respondents to the call, Age/Sex class of respondents (Adult male, Adult female, 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. β+/-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.
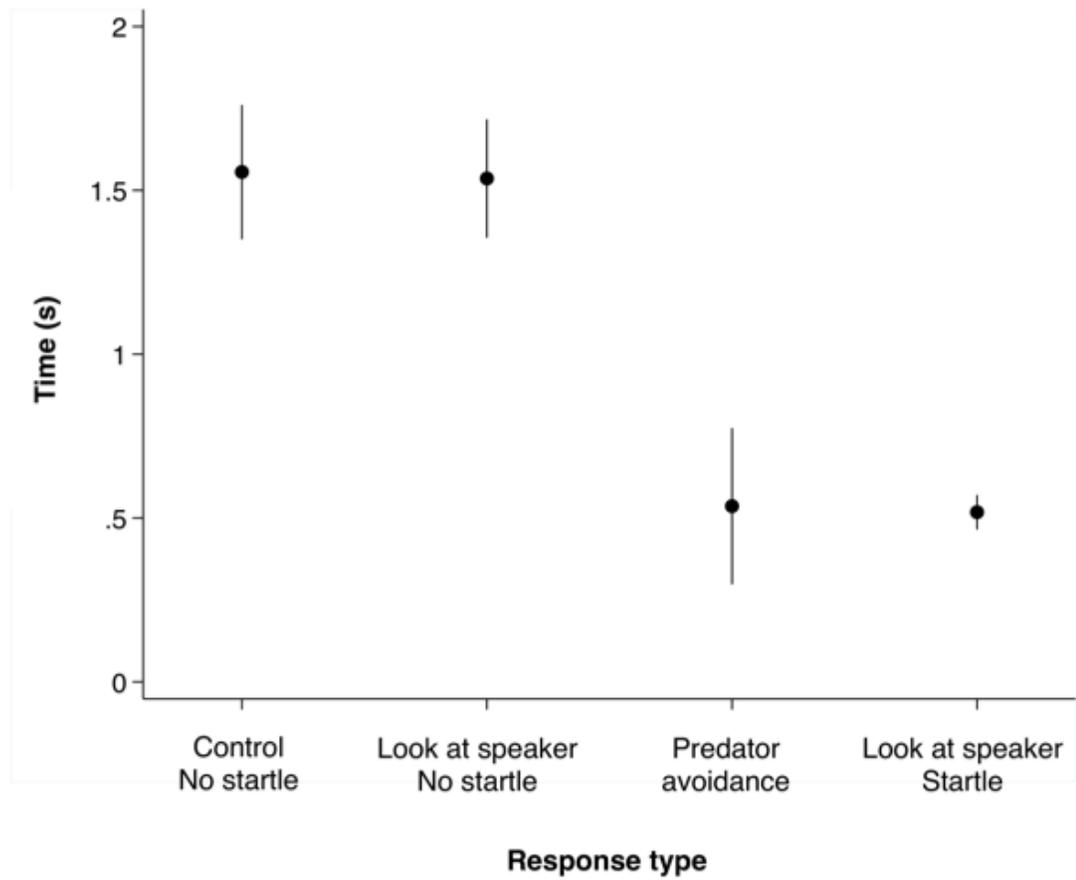
Figure 4.2: The onset time (least square mean in seconds +/- 95%CI) of the first reactions of vervet monkeys to those experimental presentation of alarm and control calls for which a response was detected.

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

Wald X^2_4=339.1, P=0.0001

Table 4.5: 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 behaviour, look at speaker with startle, look at speaker without startle). β+/-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.

Chapter 5

Discussion

My observational and experimental results accord with each other, which gives me confidence in the outcomes, but they deviate from prediction in two 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 two primary predator classes would trigger the context-appropriate behaviour specific to that predator. As such, these results make it difficult to assess the degree of stimulus independence of the calls, given that there was no overt response, for the most part, to either natural or experimental predator calls. I 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 (2010a, 2010b) suggestion that animals will be sensitive to call proximity, with greater distance indicating a lower risk of predation to the perceiver. Finally, I 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, since 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. (1980a, 1980b) 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) accords neither with Struhsaker (1967a) initial description, nor with the 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). In fact, the argument for semantic content was not derived from the invariance of the animals

responses; 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; in other words, an 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, 1980b) 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, 1980b) 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 the monkeys response should be probabilistic and reflect context; the association is therefore statistical, with a significantly higher probability of responding with the appropriate escape response when exposed to a particular predator alarm call. On a descriptive level, then, my 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, I cannot exclude the possibility that there are other differences in addition to group size that may account for this effect).

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 ($\sim$30m in both natural and experimental contexts compared to 15m in experimental contexts at Amboseli), given the negative correlation between call distance and active response. As increased inter-individual distances

result in fewer close neighbours (as indexed here by the lower number of available subjects in my trials), this may also reduce the likelihood of behavioural contagion (or response facilitation: Hoppitt, Blackburn, and Laland (2007), which would otherwise be responsible for a more uniform response across animals (i.e., animals respond to the behavioural response of a conspecific rather than to the call itself, see e.g., Armstrong (1951)). While I very rarely had the clusters of individuals that were common at Amboseli, I did once have a group of nine 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 behaviour. Interestingly, a recent study of grey kangaroos (*Macropus giganteus*) makes much the same case for a species that has no alarm calls at all (Pays, Beauchamp, Carter, & Goldizen, 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 my 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, 2010b). 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 in question nor to the animals own location in space. Given

45

Figure 5.1: A group of nine vervet monkeys (A) at the moment that the call is presented to them from a distance of 29m and (b) 300ms later. Interlacing is visible in B because images were extracted from a digital video recording.

the similarity of experimental and natural responses, together with 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 my experimental procedure. One consideration, however, has to be that I did not use snake calls in my 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 & 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 and co-workers on West African green monkeys is relevant in this respect (Price & Fischer, 2013; Price, Ndiaye, Hammerschmidt, & Fischer, 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 I see between my results and Amboseli, but it should be noted that no direct comparison with my study, nor with Seyfarth et al. (1980a, 1980b), 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, though, is that there is variability in the degree to which particular predator calls will evoke a context-appropriate response (see also Cäsar, Byrne, Hoppitt, Young, and Zuberbühler (2012)). Clearly, further work is needed, and is likely

to be valuable and revealing. The absence of snake calls in my 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 behavioural responses to predators were not prevalent in my 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., 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 I 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 (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, given that 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 & 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, my results suggest that combining a clear and well defined notion of natural meaning (Scarantino, 2010), with elements of the 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 co-variance of calls and context. Animal communication can thus consider both information and influence, as Scarantino (2010) and Wheeler and Fischer (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. In addition to 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, 1967a) and Seyfarth et al. (1980a, 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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