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Keron M. Greene

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Long-distance vocal communication in the spotted hyena, *Crocuta crocuta*

By

Keron M. Greene

A THESIS

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for the degree of

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ABSTRACT

LONG-DISTANCE VOCAL COMMUNICATION IN THE SPOTTED HYENA, *CROCUTA CROCUTA*

By

Keron M. Greene

Spotted hyenas (*Crocuta crocuta*) live in fission-fusion societies in which individuals may frequently exist at variable distances from close kin and other allies. The ability to produce long-distance vocalizations enables hyenas to advertise their location and call for assistance from individuals who may be up to several kilometers away. Here I examined long-distance vocal communication in the spotted hyena in order to elucidate sources of variation among individuals in the acoustic properties of the long distance call, and determine whether variation in these acoustic parameters influences listener response. I tested predictions of hypotheses suggesting that the use of the whoop vocalization, variation in the properties of its sound, and the response of conspecifics to this vocalization are affected by sex, age, and the context in which the call is produced. Hyenas generally whooped either spontaneously or during social excitement. Adult females and cubs usually whooped during social excitement, while adult males most often whooped spontaneously and were less likely to receive a response to their calls. Most of the observed variation in acoustic parameters was associated with the context in which the vocalization was emitted, and calls with different acoustic parameters received differential responses from conspecifics.

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Chapter 1

GENERAL INTRODUCTION

Communication is generally defined as the provision of information by a sender that can be utilized by a receiver to make a decision (Bradbury & Vehrencamp, 1998). A communicatory signal occurs because it benefits the sender to produce it. The incidental transmission of information resulting from other activities (i.e. feeding, moving, etc.) is termed a "cue". Signals may encode information about attributes of the sender, such as its motivational state, behavior, or identity, and about stimuli or events in the environment, such as location, quality, or quantity of food (Marler, 1967). Recognizing and maintaining contact with conspecifics is challenging for animals that are often separated in such a way that visual contact is no longer possible. Although other communicatory media, such as olfaction, may also be useful for long-distance communication, in most terrestrial environments sound waves are transmitted more quickly and with less signal degradation than are odors (Bradbury & Vehrencamp, 1998). Thus, when the transmission of signals is constrained by distance, individuals can still communicate efficiently through vocalizations.

Vocal signals can be described in terms of both their acoustic properties and their behavioral correlates. Acoustic properties can be defined in the frequency dimension by measuring sound frequency (pitch), amplitude, and harmonic structure (formants). The temporal structure of a vocalization includes frequency change over time, repetition of sound components (syllables), and the duration of the call. Sound can be graphically represented through plots of the change in amplitude over time (power spectrum), or frequency over time (spectrograms). Modern technological advances have made digital spectrograms and power spectra efficient methods of sound analysis (Bradbury & Vehrencamp, 1998). Observations of the behavior of animals as they produce sound, the stimuli that elicit the vocalization, and the response of receivers to the sound can offer insight into the functions of calls (Marler, 1967; Hauser, 1996).

Considerable attention has been devoted to understanding how natural selection has shaped the structure and form of animal vocal communication (e.g. Marten & Marler, 1977; Marten et al., 1977; Wiley & Richards, 1978; Waser & Brown, 1986), and various theories relating signal structure to the functions of vocalizations and their evolutionary origins have been proposed (Morton, 1977; Zahavi, 1979). Signals that contain only information about the sender's internal state are considered "motivational" (Marler, 1967). If signals provide receivers with enough information to determine the context in which the signal is produced, the signals are regarded as "referential" (Hauser, 1996). Referential signals permit listeners to predict events in their own environment. Functionally referential signals have been documented for predator calls (e.g. Seyfarth et al., 1980a; Macedonia, 1990; Evans et al., 1993) and food calls (e.g. Evans & Evans, 1999; Bugnyar et al., 2001; and review in Hauser, 1996).

In solitary species, long-distance communication might facilitate successful contacts between conspecifics during the breeding season, particularly if the information content of the message includes details regarding the sex and reproductive status of the caller. At relatively close range, brief encounters might also be facilitated if the message content of the sounds was sex- or individual- specific (Baker, 1998).

Cohen and Fox (1976) and Schassburger (1993) suggested that increasing complexity of the vocal repertoire may be indicative of social complexity, with gregarious animals possessing a larger vocal repertoire than solitary species. Short distance communication is important in many social species, and can help facilitate group movements, maintain social bonds, and provide a mechanism for individual recognition (e.g. Japanese macaques, *Macaca fuscata*: Green, 1975; vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth, 1982; ring-tailed lemur, *Lemur catta*: Macedonia, 1986; king penguins, *Aptenodytes patagonicus*: Robisson, 1992; gorilla, *Gorilla gorilla*: Seyfarth et al., 1994; Palombit et al., 1999; baboons, *Papio cynocephalus*: Rendall et al., 1999; Fischer et al., 2001; European badger, *Meles meles*: Wong et al., 1999; white-nosed coati, *Nasua narica*: Compton et al., 2001). Loud, long distance vocalizations often serve a number of different functions simultaneously. In many social mammals, these calls are used for territorial defense, mate attraction, and to maintain contact with widely spaced social companions (e.g.

wolves, *Canis lupus*: Harrington & Mech, 1979; chimpanzees, *Pan troglodytes*: Mitani & Nishida, 1993; lions, *Panthera leo*: McComb et al., 1994; Grinnell & McComb, 2001).

Here I investigate the functions of, and sources of variation in, the loud calls of one gregarious carnivore, the spotted hyena (*Crocuta crocuta*). Spotted hyenas are ideal for studies of vocal communication because they are highly vocal animals. They have the largest repertoire of any hyaenid (Kruuk, 1972, 1976; Mills, 1990; Peters & Sliwa, 1997) and a more complex vocal repertoire than most other social carnivores (i.e. wolves: Harrington & Mech, 1979; McComb et al., 1993; Schassburger, 1993; lions: Grinnell & McComb, 2001; but see African wild dogs, *Lycaon pictus*: Robbins, 2000). Spotted hyenas live in permanent groups called “clans”, which defend communal territories (Kruuk, 1972; Mills, 1990). A single clan contains multiple adult males and multiple matrilines of adult females and their offspring, who are raised at a communal den (Kruuk, 1972; Frank, 1986a; Mills, 1990). Male spotted hyenas disperse from their natal clans when they are around two years old, while females are generally philopatric (Mills, 1990; Smale et al., 1997). Each spotted hyena clan is organized on the basis of a rigid social hierarchy that influences most hyena social interactions, from feeding and hunting, to greeting ceremonies and sexual behavior (Frank, 1986b; Holekamp & Smale, 1991; Szykman et al., 2001; Engh et al., 2002). Hyenas live in fission-fusion societies in which close kin or other important social allies may not be present in an individual’s immediate vicinity. The ability to produce long-distance vocalizations enables hyenas to advertise their location and call for assistance from individuals who may be several kilometers away. The fluid nature of hyena social groups and the complexity of the social environment provide ideal conditions for the development of a complex long-distance communication system.

Chapter overview

Chapter 2 begins with a review of the current literature on spotted hyena vocalizations, and a description of the vocal repertoire. I then investigated the sources of variation in spotted hyena whoop vocalizations, and asked whether the social context in which whoops are emitted affects the structure of the vocalization produced. I also asked whether whoops with different acoustic properties elicited different responses from listening conspecifics. This level of vocal complexity has not been examined in spotted hyenas, and provides necessary insight into the role of long distance communication in this species.

In Chapter 3, I examined the possibility of exploiting long-distance vocalizations to determine clan territorial boundaries by using playback techniques (i.e., call-ins) to attract animals to a particular location and monitor them for territorial behaviors. Call-ins have been used successfully to determine the size of hyena populations (Kruuk, 1972; Creel & Creel, 1996; Mills, 1996; Ogutu & Dublin, 1998; Mills et al., 2001), also might potentially offer an efficient method of mapping clan divisions within a geographical area.

Data in Chapter 2 were collected from a single spotted hyena clan, the Talek clan, which defends a territory on the northeastern edge of Kenya's Masai

Mara National Reserve. The Talek clan has been studied intensively since 1988, and Dr. Kay Holekamp, Dr. Laura Smale, their field assistants, and graduate students working on the Mara Hyena Project, collected much of the data presented here. The audio recordings and field data analyzed here are the result of years of careful observation by many people. The data presented in Chapter 3 are the result of a series of field experiments I conducted between May and August 2000, which could not have been completed without the researchers on the Mara Hyena Project. Erin Boydston provided GIS maps and expertise essential in documenting hyena responses to the call-ins. Therefore, I use the term "we" throughout each chapter to indicate that my thesis research was a collaborative effort.

Each of these chapters examines long-distance communication in the lives of spotted hyenas. In Chapter 2, I found that much of the variation observed in the acoustic structure of spotted hyena whoops results from the influence of the caller's social environment at the time of the whoop. I also found a difference in the likelihood of hyenas responding to a whoop based on the identity of the caller and the context in which the caller vocalized. These data suggest that spotted hyena whoops are complex signals, which contain extensive information that can be used by receivers to determine their responses, and provide a mechanism for maintaining group cohesion over long distances. My results also suggest a relationship between whoops and individual vocal recognition in this species. The results of Chapter 3 indicate that while call-ins may someday prove to be a useful tool for censusing hyena populations and determining their space-use patterns, the technique needs refinement.

Chapter 2

LONG DISTANCE VOCAL COMMUNICATION IN THE SPOTTED HYENA

Introduction

Recent research on animal vocal communication has focused on determining the functions of calls by elucidating the information they convey to recipients. Most researchers judge the meaning of calls based on the responses they elicit from listeners (e.g. Snowdon et al., 1983; Seyfarth et al., 1994; Rendall et al., 1999). It has been argued that animal signals are both motivational and referential, containing information about both the internal state of the caller and the external environment (e.g. Marler et al., 1992). Minor modifications of a single call type can result in different messages without the need to develop new call production and reception mechanisms (Cleveland & Snowdon, 1982). Call subtypes in which different meanings are conveyed by acoustic variation are also advantageous since they allow recipients to decipher signal meaning without using visual cues. In many species of nonhuman primates (e.g. Seyfarth et al., 1980a; Cheney & Seyfarth, 1982; Fischer, 1998), vocalizations have been described that elicit different responses depending on the call subtype produced, suggesting that these calls might have meanings associated with their acoustic structure. In some species, the structure of a particular type of call can be affected by the circumstances under which it is emitted (Norcross & Newman, 1993; Norcross et al., 1999; Rendall et al., 1999).

While variation in vocalizations and their association with behavioral contexts has been extensively studied in primates (e.g. Green, 1975; Hauser, 1991; Norcross & Newman, 1993; Hammerschmidt & Todt, 1995), relatively little research of this nature has been done on other animals (Brown & Farabaugh, 1997; Jennings et al., 1997; McCowan & Reiss, 2001; but see Insley, 1992). The present study documents variation in acoustic structure and the role of call context in the long-distance vocalization of one gregarious carnivore, the spotted hyena (*Crocuta crocuta*). The spotted hyena is a highly vocal species that produces a rich repertoire of sounds. These animals live in a fission-fusion society in which an elaborate vocal communication system appears to allow group members to maintain social bonds, both within the immediate vicinity and also with conspecifics out of visual range (Kruuk, 1972). Kruuk (1972) identified eleven vocalizations in this species, and briefly described the circumstances under which each call was emitted (Table 2.1).

Spotted hyenas live in social groups (called "clans") structured by rigid, linear dominance hierarchies (Kruuk, 1972; Tilson & Hamilton, 1984; Frank, 1986b; Mills, 1990). Although the hierarchical dominance relationships among *Crocuta* clan members closely resemble those characteristic of many old-world primate societies, they are unique among social carnivores (Ewer, 1973; Holekamp et al., 2000). Kruuk (1972) suggested that most spotted hyena vocalizations contained either submissive or aggressive messages, and assigned

Table 2.1 *Descriptions of spotted hyena vocalizations, their associated physical characteristics, and the contexts in which they are typically observed. Modified from Kruuk (1972)*

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Name of vocalization	Description of sound	Posture	Situation
Whoop	Series of calls; -ooo- tone, each call beginning low ending high, some calls may be low-high-low. Last call of series often reduced to only the low-pitched part. Very loud, may be heard more than 5km away.	Emitted walking, standing, or lying. For each call in series mouth opened slightly, with muzzle near ground.	Emitted by both sexes, either alone or in company. Rarely "answer" each other's calls; whoops often appear to be spontaneous, without external cause.
Fast whoop	As above, calls and intervals shorter, not "petering out"	Tail horizontal or high, ears cocked; often running; mouth as above near ground	With many other hyenas present, often in confrontation over kill with lion or other clan; often just before a group of hyenas attacks together.
Grunt	Soft, very low-pitched growling sound, lasting several seconds.	Mouth closed, aggressive posture.	Emitted on approach of another hyena, often followed by chasing.
Groan	Low-pitched -mmm- sound, lasting intermittently for up to 15 sec.	Head low, mouth closed or slightly open, often while engaging in greeting.	Emitted just before and during greeting ceremony, by females to call cubs out of the den, or while sniffing cubs.
Low	Cow-like sound with pitch varying during call, usually low-pitched, lasting several seconds.	Mouth slightly open, head rather low but usually horizontal.	As with fast whoop, but less likely to lead to immediate attack.

Name of

Name of vocalization	Description of sound	Posture	Situation
Giggle	Loud, very high-pitched and rapid series of hee-hee-hee, usually shorter than 5 sec. Reminding one of human "mad laughter."	Running away in fleeing posture. Mouth slightly open, often grinning.	When attacked or chased, often over a kill.
Yell	Loud, with varying but high pitch, lasting up to a few seconds, like a human yell in response to pain.	As with giggle, or defensive posture.	As with giggle, usually when actually being bitten; stronger tendency to flee than with giggle.
Growl	Loud, with varying but low pitch, lasting up to several seconds, with -aaa- and -oh- tones, often with a rattling quality in it.	Defensive posture.	When attacked and bitten, often when about to bite back, loudest when actually returning a bite.
Alarm rumble	Rapid succession of low-pitched, soft staccato grunts in a series lasting several seconds.	Mouth closed or slightly open. (a) In fleeing posture, (b) or standing with tail horizontal or high, ears cocked.	When alarmed when at the den or on a kill. In encounters between clans or between hyenas and lions over kills, or at the approach of a lion or human.
Squitter	Loud, high-pitched, long drawn-out squeals of -eee- sounds, often with a staccato element (-ee-ee-ee-ee-), very rapid. May continue for minutes with short breaks.	Mouth slightly open, tail hanging down, head rather low.	By cubs when following a female before suckling, or when thwarted in attempts to get food from a kill.
Soft squeal	As squitter, but soft, no staccato, lasting several seconds.	Mouth slightly open, ears flat, head often tilted slightly, teeth bared, often rolling over on side.	By cubs, but also adults; when meeting a well-known individual after long separation.

possible functions to each call. The loud calls of the spotted hyena (yells, giggles, whoops) are the most well known and recognizable. Yells and giggles are usually given after an individual has been attacked and are generally submissive calls, but the function of whoops and their eliciting stimuli are poorly understood (Kruuk, 1972; Mills, 1990).

The spotted hyena whoop is a high-amplitude call with fundamental frequencies ranging between 200 and 375 Hz (East & Hofer, 1991a). Multiple discrete calls are produced in bouts of sound that can travel distances of five kilometers or more (Kruuk, 1972). Kruuk (1972) identified two types of whoops, slow and fast, which he distinguished based on the rate at which individual calls were produced within a bout (Figure 2.1). East and Hofer (1991a) provided the first systematic technical description of this vocalization, documenting its acoustic structure, structural variation in whoops among individuals, and ontogenetic changes in whoop structure within individuals. They identified three distinct types of whoops, designated "A", "S", and "T", which differ from one another in structure and sound. In high quality recordings, these types are easily distinguished acoustically and by visual inspection of spectrograms (Figure 2.2). Type A (asymmetrical) whoops contain an initial low frequency section followed by an abrupt rise. Type S (symmetrical) whoops begin with a low frequency section, rise in pitch, and then return to the initial low frequency. Type T (terminal) whoops are lowing sounds characterized by little change in frequency, and they are always found at the end of a bout. Bouts typically contain combinations of all three types, however longer bouts tend to contain higher

Figure 2.1. Spectrograms illustrating examples of Kruuk's (1972) (a) "slow" and (b) "fast" whoop bouts. The whoop rate of (a) is 10.8 whoops/min, while that of (b) is 39.2 whoops/min. These whoops were produced by (a) adult male MIKE, and (b) female cub MALI.

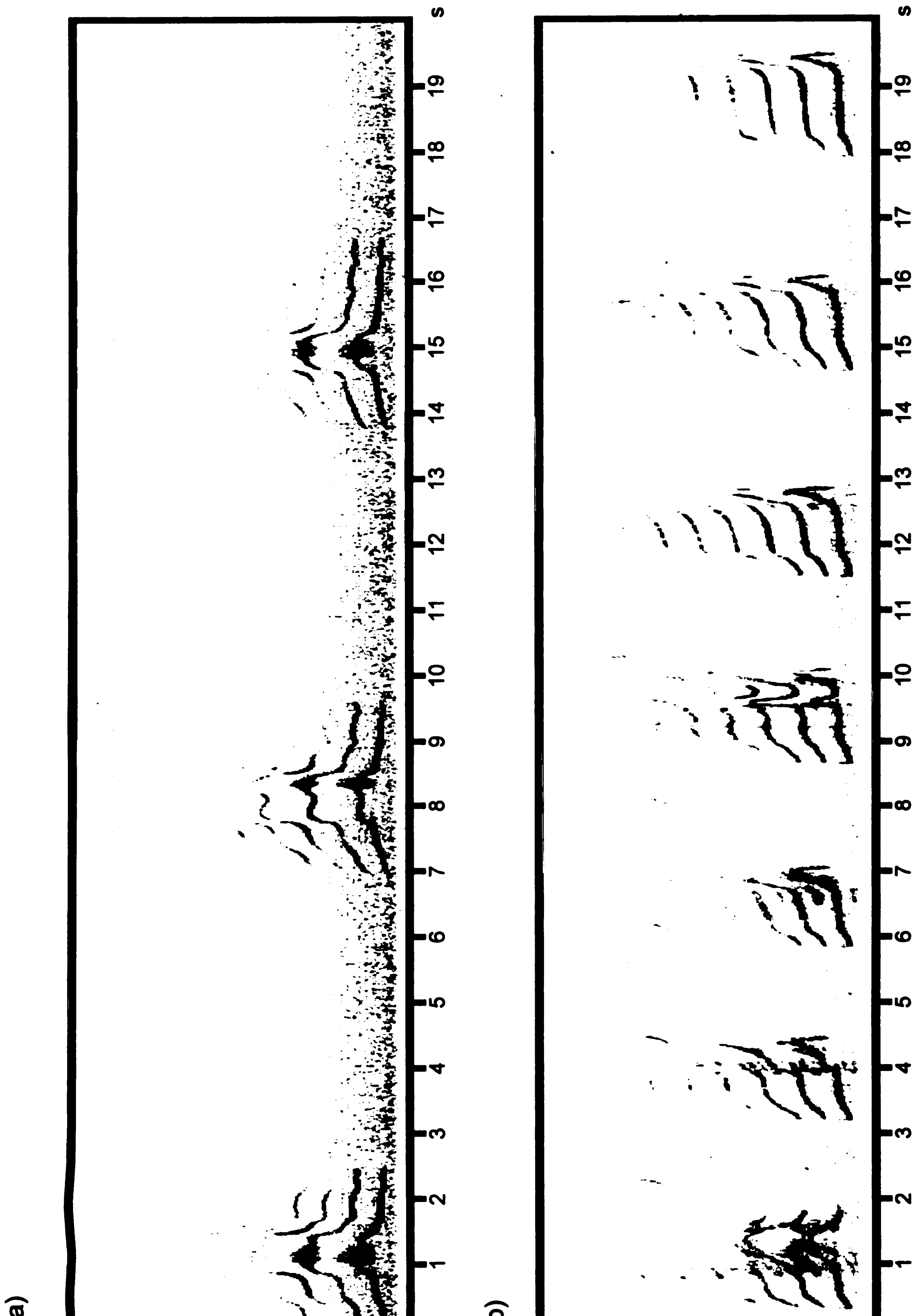
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Figure 2.2 Spectrograms illustrating Type A (a), Type S (b), and Type T (c) whoops. Three examples of each whoop type are shown, with samples from cubs (top), adult males (middle), and adult females (bottom). These whoops were emitted by nine different individuals. (across from top left: cubs DNA, ALI, CUJ; adult males RCN, FA, MIKE; adult females JAB, NAV, GER)

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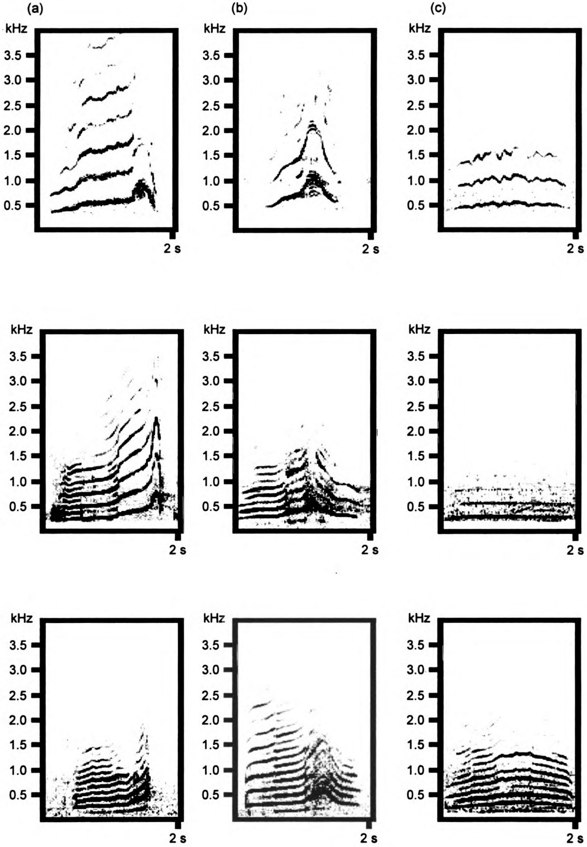


percentages of Type A whoops. Male and female spotted hyenas of all ages produce all three whoop types. East and Hofer (1991a) suggested that the high frequency portion found in whoop Types A and S may allow hyenas to determine the direction from which the call is coming, while the low frequency portions of may reduce attenuation and enhance long-distance sound transmission.

Spotted hyenas of both sexes begin to whoop during the first month of life (East & Hofer, 1991a), and continue to do so in a variety of circumstances, often with no observable stimulus prompting them to vocalize. Hyenas can whoop while standing, walking, loping, or lying down (Kruuk, 1972; Mills, 1989; East & Hofer, 1991a). Typically a spotted hyena lowers its mouth toward the ground during the initial low frequency section of a whoop (Figure 2.3), and at most raises its head to roughly the same plane as the animal's back as the high frequency section is produced, regardless of its posture before whooping. The head is never pointed skyward while the hyena whoops, as occurs during howling by wolves (Harrington & Mech, 1979).

Sound frequencies change over the course of a single whoop, and there is a great deal of variation among individuals with respect to temporal patterning. However, since the basic acoustic structure of the call remains stable within individuals over time, spotted hyenas may be able to use these variable acoustic cues to locate and identify specific callers, and to assess the caller's motivational state (Waser & Waser, 1977; McGregor & Krebs, 1984; Mills, 1989; East & Hofer, 1991a, b). Calls with more frequency modulation facilitate better

Figure 2.3 Two of the postures assumed by spotted hyenas at the beginning of a whoop. (top) An adult male whooping while walking. (bottom) A cub whooping while standing still. Photos courtesy of Anne L. Engh (top) and Kay E. Holekamp (bottom).

localization (Bradbury & Vehrencamp, 1998) and the rate at which whoops are produced, as well as variation in the range of frequencies, may reflect the caller's motivational state (Kruuk, 1972; Eisenberg, 1976; Morton, 1977; Mills, 1990). If variation in the acoustic structure of whoops communicates what is happening to the caller, then the sound produced ought to vary with the circumstances under which the vocalization is emitted. Although East and Hofer (1991b) described the situations in which hyenas whoop, and the average composition of whoop bouts for each age and sex class, they did not describe how acoustic variation in the vocalization relates either to the caller's immediate circumstances or to the responses of conspecific listeners. The present study inquires whether the context in which a whoop bout is emitted influences the structure of the whoops within a bout, and whether the responses of conspecifics vary with the acoustic structure of whoops.

Methods

Study animals

This study was conducted in the Talek area of the Masai Mara National Reserve, in southwest Kenya. This is an area of open, rolling grasslands grazed year-round by large concentrations of ungulates. The subject population was one large *Crocuta* clan inhabiting a home range of approximately 65 km^2 (Frank, 1986b; Boydston, 2001). All members of the Talek clan were identified by their unique spot patterns and other conspicuous characteristics, such as ear notches, and the sex of each individual was determined from the dimorphic glans morphology of the erect phallus (Frank et al., 1990). Birth dates were assigned to cubs by estimating their ages when first observed above ground at natal or communal dens. Cub ages could be estimated to within seven days based on their pelage, size, and other aspects of their appearance and behavior. In this study, hyenas were considered juveniles until they were 24 months of age, and older animals were classified as adults. Genealogical relationships were as described by Holekamp et al. (1993), and mother-offspring relationships after 1993 were assigned based on regular nursing associations.

Continuous monitoring of the study clan began in 1988, and the information used for this study was extracted from a data set of observations made between 1988 and 1998. Observers were present in the study area at least 23 days per month, except during April 1991, when observers were present on only 14 days. The activities of Talek hyenas were monitored from vehicles, which were used as mobile blinds. An observation session started when one or more hyenas were found separated from other hyenas by at least 200m, and ended when these animals moved out of sight (as when entering bushes) or when observers left the area. Observations were made at natal and communal dens, at ungulate kills, and away from both dens and kills (e.g., when animals were traveling or resting). Following Altmann (1974), all occurrences of agonistic interactions, affiliative behaviors, and arrivals or departures of hyenas were recorded as critical incidents. Recorded agonistic behavior included both the aggressive behavior of the initiating individual, and the response of its victim.

Contexts in which whoops were emitted

From 1995 to 1998, field researchers studying the Talek clan recorded whoops during routine observation sessions using a Marantz PMD-22 portable cassette recorder and a Sennheiser ME66 directional microphone. For each whoop bout recorded, caller identity, date and time, location, social context (see below) at the time of the whoop, and maximum sound pressure were noted. The resulting sound library consisted of recordings of whoops produced by hyenas of all ages, in various social contexts, and found at all observation locations. For the majority of recorded vocalizations, detailed information was available describing events occurring during the time periods immediately before and after each whoop. We also documented the type and intensity of behavior displayed in response to specific whoop bouts by all animals present, as well as the identities of the animals involved. Additional information for whoops that had not been tape-recorded was collected following the same procedure, using archived field notes. In all cases, whoop bouts were only examined if there were at least 10 minutes of behavioral observations available both prior to and following the whoop, and if there were no other vocalizations occurring during the 10 minute intervals before and after the whoop.

We assigned all whoops emitted by Talek hyenas to one of three general social contexts: *1) During general excitement.* Whoops sometimes occurred when the caller (and frequently the entire social group) was exhibiting a high level of excitement. Such situations included instances when the caller behaved aggressively toward another individual, when the caller had just been the target of aggression by a conspecific, when the caller was a bystander to aggression directed toward a third hyena, or when the caller's group was involved in a confrontation with lions or members of a neighboring clan. Hyenas exhibit excitement by holding their heads up, their ears forward, and their tails elevated, erect, and bristled (Kruuk, 1972). *2) Spontaneously.* Hyenas were often observed whooping when there was no apparent stimulus eliciting the call. For example, hyenas whooped when they were alone or when they were with other hyenas but no social or interspecific interactions were occurring. Individuals also frequently whooped when approaching or leaving a group of conspecifics in which nothing was happening to generate social excitement. Thus these whoops were also classified as occurring "spontaneously." *3) Following a greeting.* Spotted hyenas often engage in a greeting ceremony when they encounter another clan member (Kruuk, 1972; East et al., 1993). Upon meeting, the two hyenas stand head-to-tail, lift the rear leg closest to the other hyena, and sniff one another's genitals. Here we noted whether one member of a greeting pair whooped immediately following the greeting. Preliminary analyses suggested that whoops produced after greeting may share similarities to whoops produced spontaneously and during excitement: with respect to whoop rate, whoop duration, and inter-whoop interval they were not significantly different than either spontaneous or excited whoops. Because greeting contexts contained similarities to contexts involving both spontaneous whoops and those emitted during social excitement, and because whooping following a greeting was rare (n=13), we excluded whoops following greetings from all analyses involving context.

Responses to whoops

All hyenas within a 5 km radius from the caller were considered to be within range of the sound (Kruuk, 1972). The events we observed following a bout were assigned to one of two general categories, those in which there was an unambiguous reaction exhibited by one or more listeners, and those in which there was no significant response from any observable conspecifics within acoustic range. Behavior of conspecifics that heard whoops was variable. An approach to within 1m of the animal that just whooped, social interaction with the caller, or the arrival on the scene of hyenas not originally present was considered a reaction to the vocalization. However a mere change in body or head orientation toward the animal that just whooped was categorized together with cases in which all listeners appeared to ignore the caller completely.

In order to determine whether the arrival of new hyenas to the scene, and/or the approach of a hyena to the caller, could indeed be considered responses to a whoop, we compared the rates of arrivals and approaches observed before and after each whoop using the Wilcoxon Signed-Ranks test. We examined archived field notes containing observations made between January 1995 and December 2001 for all instances in which an identified hyena emitted a whoop. We examined behaviors occurring during ten-minute intervals before and after the beginning of the whoop bout. The identity of each responding hyena was noted, as well as the nature of any interaction it had with the caller, if any occurred. We rejected any instance in which there were less than ten continuous minutes of observations before or after the vocalization, when another whoop occurred during the ten minutes both before and after, and if the "pre-whoop" period overlapped with the "post-whoop" period of a previously occurring vocalization. We also eliminated any instance in which the caller whooped as it was arriving to or departing from a scene. While hyenas frequently whooped in these contexts, these instances were disregarded for the purposes of this analysis in order to minimize any potential bias resulting from the absence of the caller from the scene.

In total 85 instances were examined from archived field notes. We recorded the caller's id, the context of the vocalization (excitement, greeting, or spontaneous as previously described), the time relative to the whoop of an arrival or approach, and the identity of the arriving or approaching animal. Approaches included conspecifics moving to within 1 meter of either the caller or the individuals who had been interacting with the caller (as in maternal interventions or assistance against an aggressive individual).

Previous studies have shown that vocal recognition of maternal kin occurs among hyenas with *r*-values as small as 0.125 (Holekamp et al., 1999). Therefore, for analyses of the relationship of each responding hyena to the caller, we defined kin as maternal relatives having an *r*-value of 0.125 or greater. Since paternity information was not available for all individuals sampled here, we did not consider paternal kin in this analysis.

Digital sound analysis

Recorded whoops were digitized at a sampling frequency of 12 kHz using a 16-bit mono audio format. Spectrograms were generated using the Avisoft-SASLab Pro software package (Specht, 2000) with a Hamming window and an FFT length of 512. We measured six acoustic features: bout duration, number of whoops per bout, the duration of each whoop, the duration of each inter-whoop interval, and fundamental frequency (Figure 2.4). Bout duration was defined as the number of seconds between the beginning of the first whoop in the series and the end of the last whoop in the series. The number of whoops per bout was determined by counting the discrete calls within each bout. Whoop duration (in seconds) was measured for each call within the bout, and the inter-whoop interval was determined by measuring the number of seconds elapsed between the end of one call in a bout and the beginning of the next call. The acoustic frequency varies from the beginning to the end of a whoop, and each whoop type (A, S, T) has an inherently different pattern of frequency change. Therefore, the fundamental frequency was considered to be the lowest frequency at the beginning of a whoop. We measured this frequency using digital spectrograms (Figure 2.4). Measurements were not taken from partial recordings or those that produced indistinct spectrograms. We calculated the whoop rate (number of whoops per minute) within a bout, the mean duration of whoops within a single bout, and the mean duration of inter-whoop intervals within each bout.

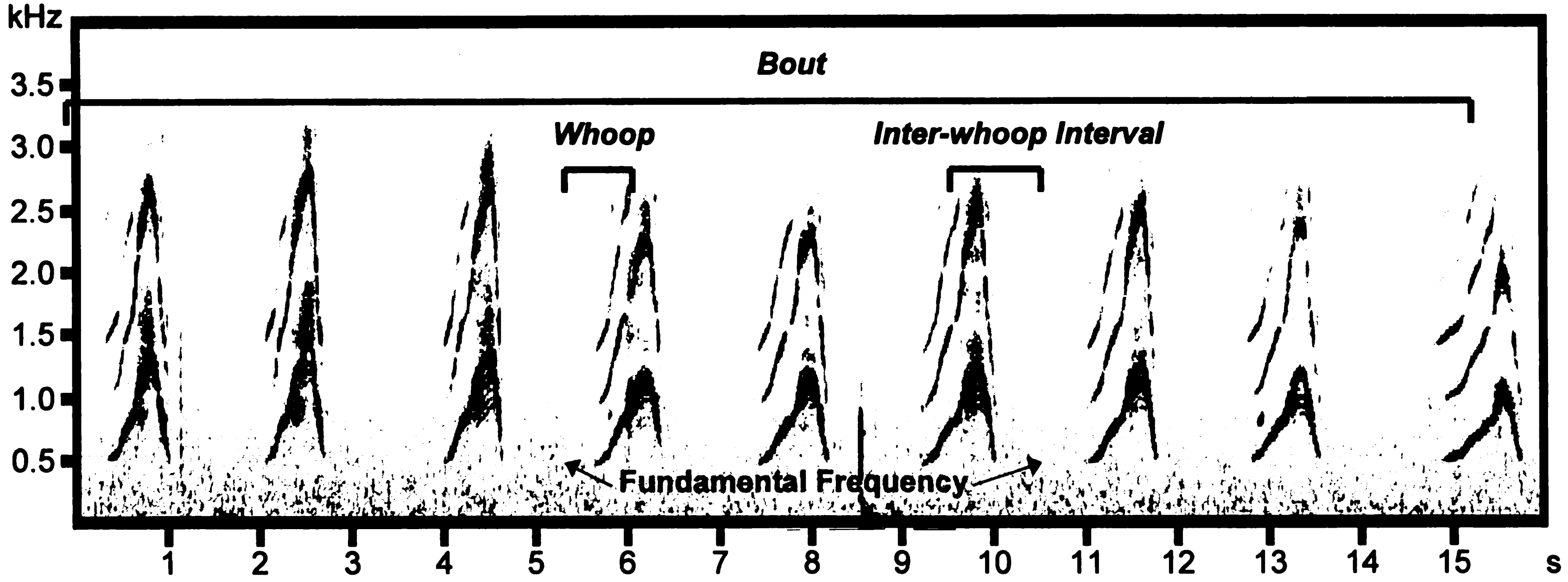


Figure 2.4 Spectrogram of a spotted hyena whoop bout showing four of the measures obtained. The durations of individual whoops and inter-whoop intervals were measured and averaged to give mean values for the bout. This bout was emitted by male cub DYL.

Data analysis

A context, as well as whether or not any response occurred was recorded for each of 112 digitized whoop bouts, as were measurements of their acoustic parameters. Behavioral observations of 85 whoops drawn from additional sessions in archived field notes but not associated with a sound recording were used in analyses of context and response. Data were analyzed using Chi-square, Mann-Whitney U, or Wilcoxon Signed-Ranks tests. Mean values were presented ± standard errors. Statistical significances for multiple comparison tests were calculated using the sequential Bonferroni method (Rice, 1989), and the resulting adjusted critical values presented with the test statistic. All other differences between groups were considered significant when $P \leq 0.05$. All analyses were performed using SYSTAT version 8.0 software package (SPSS, Inc.).

Results

Variation in fundamental frequency

The fundamental frequencies of whoops from Talek hyenas ranged from 597 Hz in the youngest cubs to 128 Hz in adult females (Figure 2.5). As cubs mature, their voices deepen steadily until at least 24 months of age ($R^2=0.678$, $F_{1,71}=149.226$, $p<0.0001$). As females age, their voices deepen, reaching adult pitch around 50 months of age. Male hyenas disperse into a new clan sometime

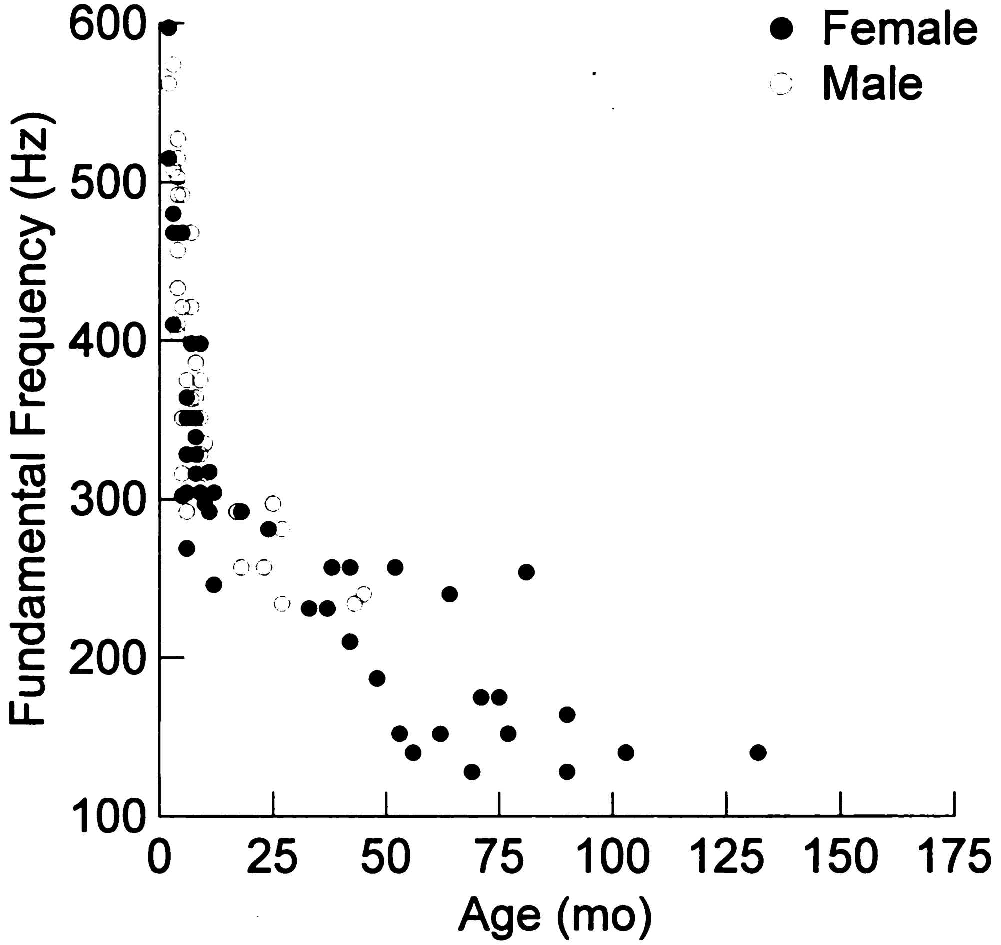


Figure 2.5 Fundamental frequencies of spotted hyena whoops. Most adult males were excluded since their exact ages were unknown. However, samples from a few adult natal males who had not yet dispersed were included.

after reaching reproductive maturity at 2 years of age (Smale et al., 1997), and therefore few of our recorded whoops were emitted by adult males of known age (n=5). However, we were able to compare the fundamental frequencies of adult males and females using recordings of adult immigrant males (Figure 2.6). Among both adults and cubs, whoops produced by females had significantly lower fundamental frequencies than whoops produced by male peers (adults: Mann-Whitney U=142, p<0.0001; cubs: U=378, p=0.016; Figure 2.6). There was no effect of context on fundamental frequency for any sex/age group (adult female: U=22.5, p=0.145; adult males: U=48, p=0.769; female cubs: U=13.5, p=0.202; male cubs: U=97, p=0.824).

Contexts in which whoops occurred

Behavioral data and clear digital spectrograms were available for 131 whoop bouts representing samples from 62 individual hyenas (mean = 2.113 ± 0.25 bouts per individual). The context in which the whoop bout was emitted could not be determined with certainty in 19 cases. Data from these 19 recordings were used only in analyses that did not require contextual information. For the remaining 112 recordings, average values for all 5 acoustic parameters (number of whoops, bout duration, whoop duration, mean inter-whoop interval, and whoop rate) were calculated when there were multiple whoop bouts emitted in the same context by any individual hyena. This resulted in 77 cases with known context and a sound recording. For analyses of whoop context that required behavioral information but not spectrographic data, archived

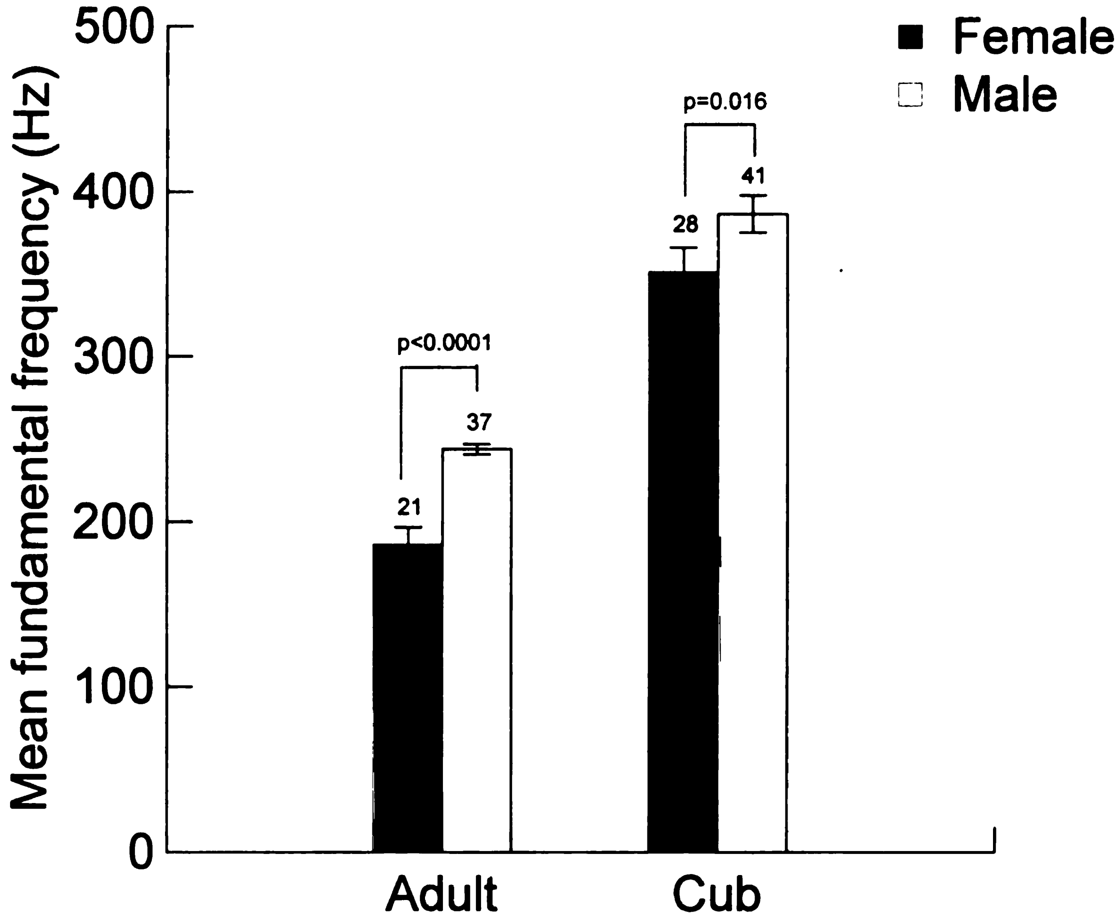


Figure 2.6 Mean (± SE) fundamental frequencies for hyenas in each age/sex group. Adult males included both adult natal and immigrant males. Numbers over bars represent the number of individuals sampled in each age/sex class.

observations (n=85 individuals) were examined to determine the context of additional bouts in order to supplement the information gained from the audio recordings.

The probability of whooping in a given context varied among sex/age groups (n=145, X^2_3=32.211, p<0.0001, P≤0.01; Figure 2.7). Male and female cubs were equally likely to whoop in both contexts (n=77, X^2_1=0.978, p=0.323, P≤0.025), and were grouped together for subsequent analyses of whoop contexts. Adult male hyenas were more likely to whoop spontaneously, and less likely to whoop during social excitement, than either adult females (n=68, X^2_1=22.838, p<0.0001, P≤0.017) or cubs (n=116, X^2_1=27.905, p<0.0001, P≤0.013). There was no significant difference between adult females and cubs in the likelihood of whooping spontaneously or during excitement (n=106, X^2_1=0.040 p=0.842, P≤0.05).

Variation in whoop rate

The frequency distribution (Figure 2.8) of the whoop rates of all bouts sampled (n=131) demonstrates a continuous range of whoop rates, rather than the bimodal "fast" and "slow" whoop types suggested by Kruuk (1972). The rate at which whoops are produced in a whooping bout (whoop rate = number of whoops/min) might be affected by changes in either the duration of the whoops themselves, the duration of the interludes between the whoops (inter-whoop

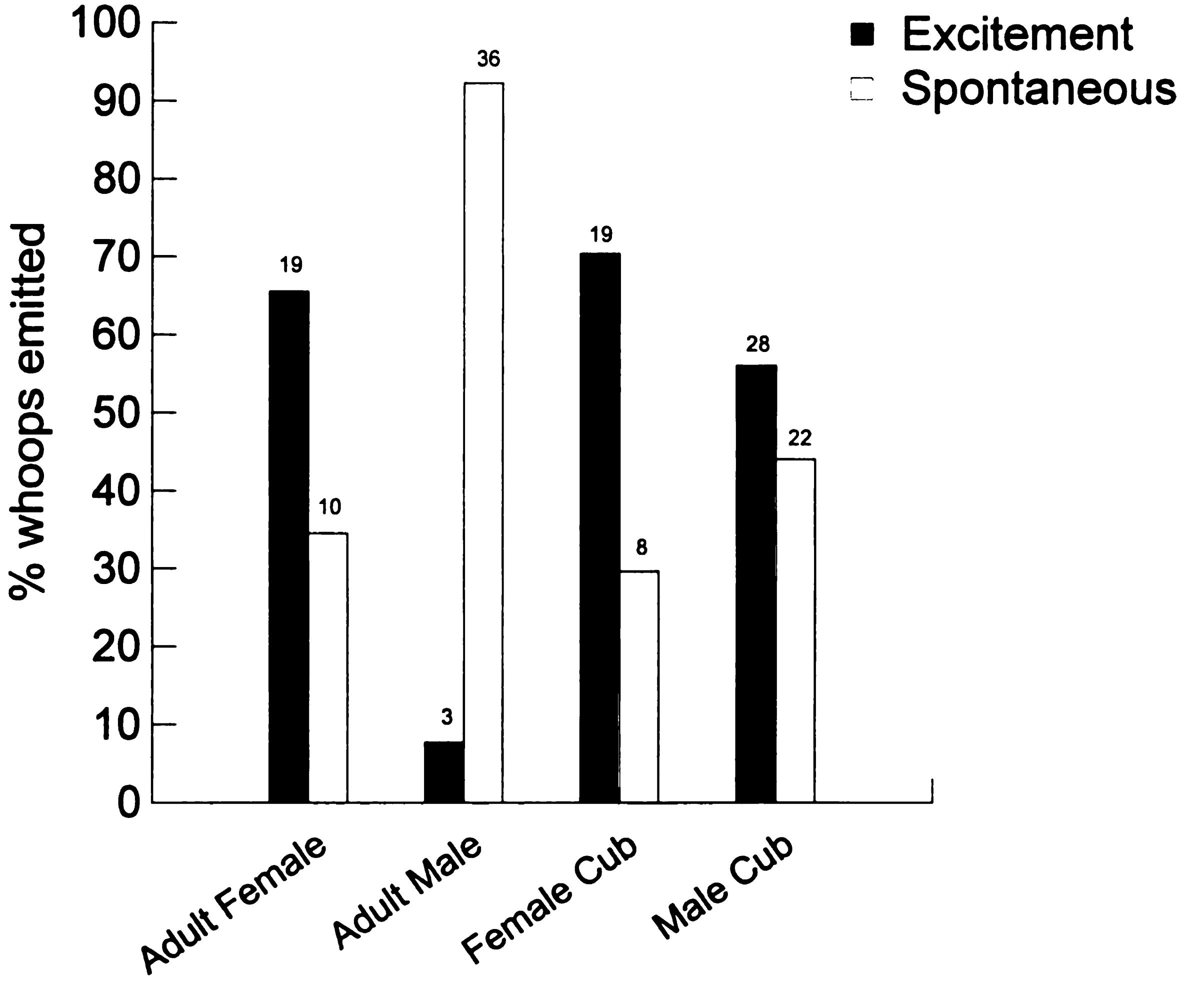


Figure 2.7 Whoop distributions for each context by sex and age class. Numbers over bars refer to the number of individuals emitting whoops in the indicated context.

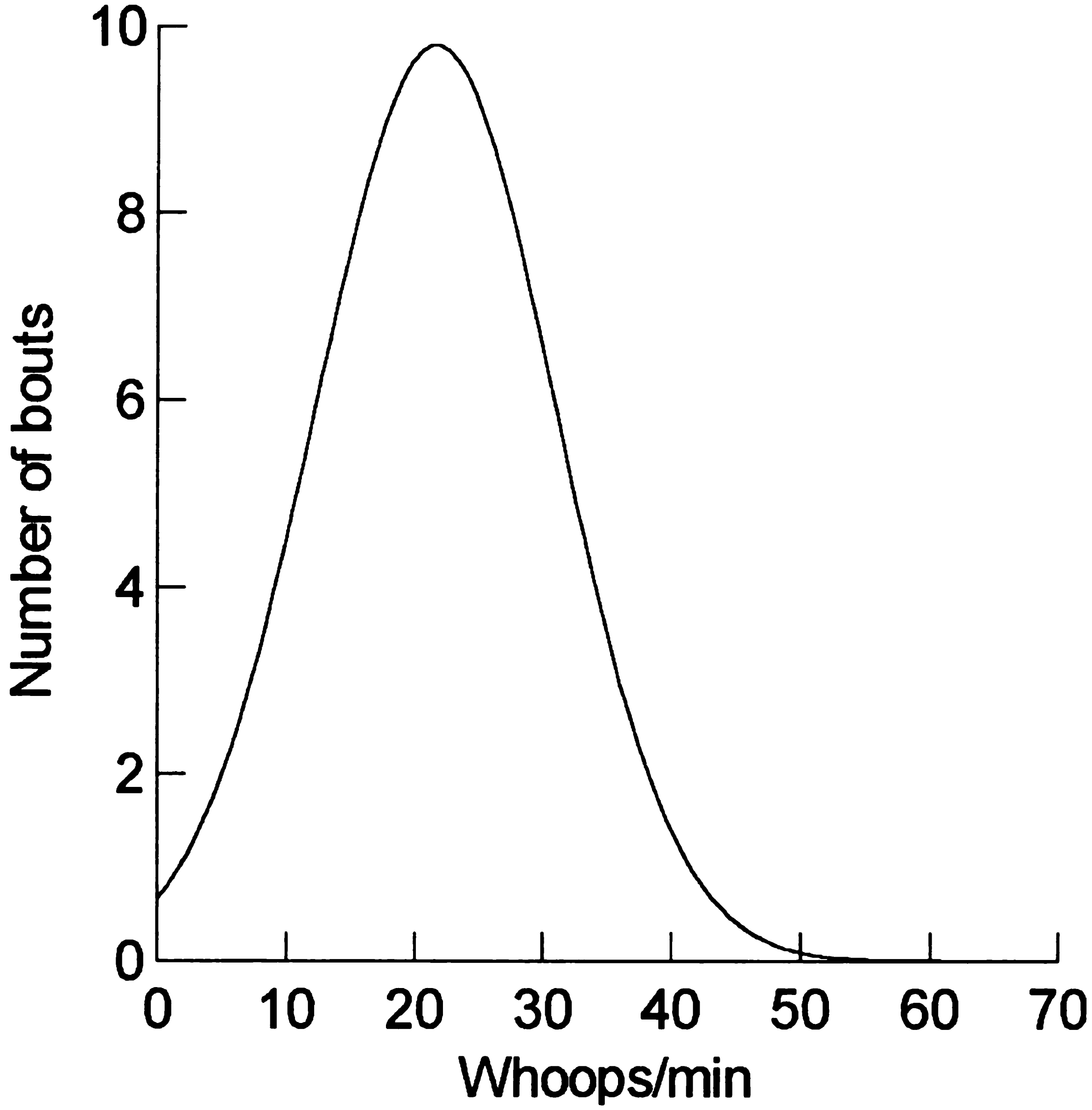


Figure 2.8. Frequency distribution for the whoop rates of all sampled bouts (n=131).

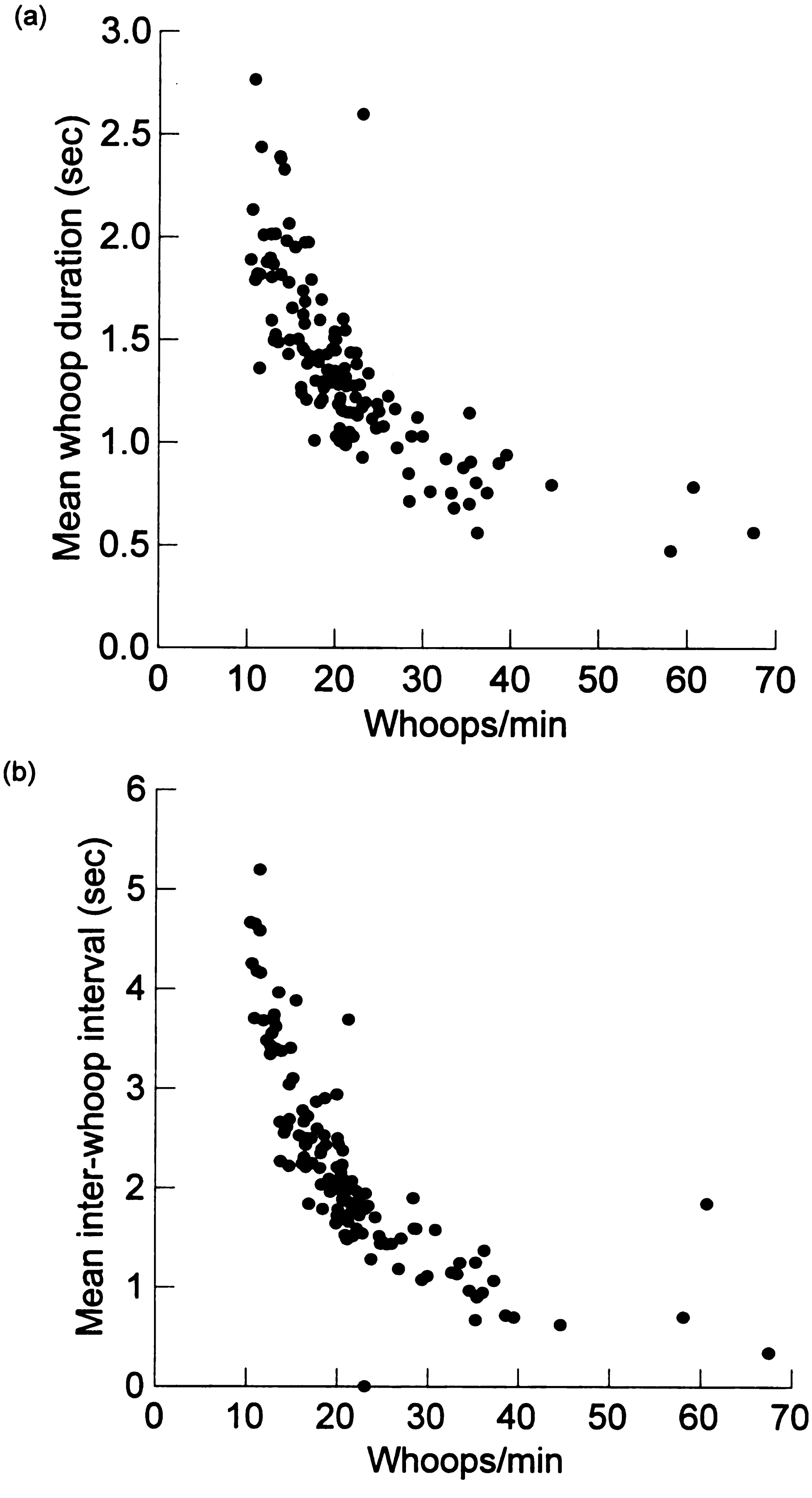
intervals), or both parameters. In fact, higher whoop rates were associated both with shorter whoop durations and with shorter inter-whoop intervals ($F_{2,124}$=260.665, p<0.0001, whoop duration: r_p= -0.718; inter-whoop interval: r_p= -0.730; Figure 2.9).

Effects of sex, age, and context on bout parameters

There were significant effects of age and context on whoop rate (age: Mann-Whitney U=246, p<0.0001; context: U=878, p<0.0001; Figure 2.10). There was no effect of the sex of the caller on whoop rate (U=629, p=0.232). Cubs whooped faster than adults in spontaneous contexts (U=30, p=0.001), but there was no significant difference based on age during social excitement (U=96, p=0.072). Whoop rates were faster during social excitement than in spontaneous contexts for both adults (U=245, p=0.002) and cubs (U=169, p=0.015).

The mean duration of whoops within a bout was affected by both age and context (age: U=811, p=0.001; context: U=276, p=0.001 Figure 2.11), but not by sex (U=547, p=0.892). Adults produced longer whoops than cubs when whooping spontaneously (U=169, p=0.015), but there was no significant difference between adults and cubs for whoops produced during social excitement (U=200, p=0.096). The duration of adult whoops were shorter when whooping during social excitement than spontaneously (U=87, p=0.036), but there was no significant difference in the length of whoops produced by cubs in the two contexts (U=65, p=0.063).

Figure 2.9. Relationship between whoop rate and (a) the duration of individual whoops within the bout, or (b) the duration of inter-whoop intervals. Higher whoop rates are produced by shortening both whoop durations and inter-whoop intervals.


(a)
Mean whoop duration (sec)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
10
20
30
40
50
60
70
Whoops/min
(b)
Mean inter-whoop interval (sec)
6
5
4
3
2
1
0
0
10
20
30
40
50
60
70
Whoops/min

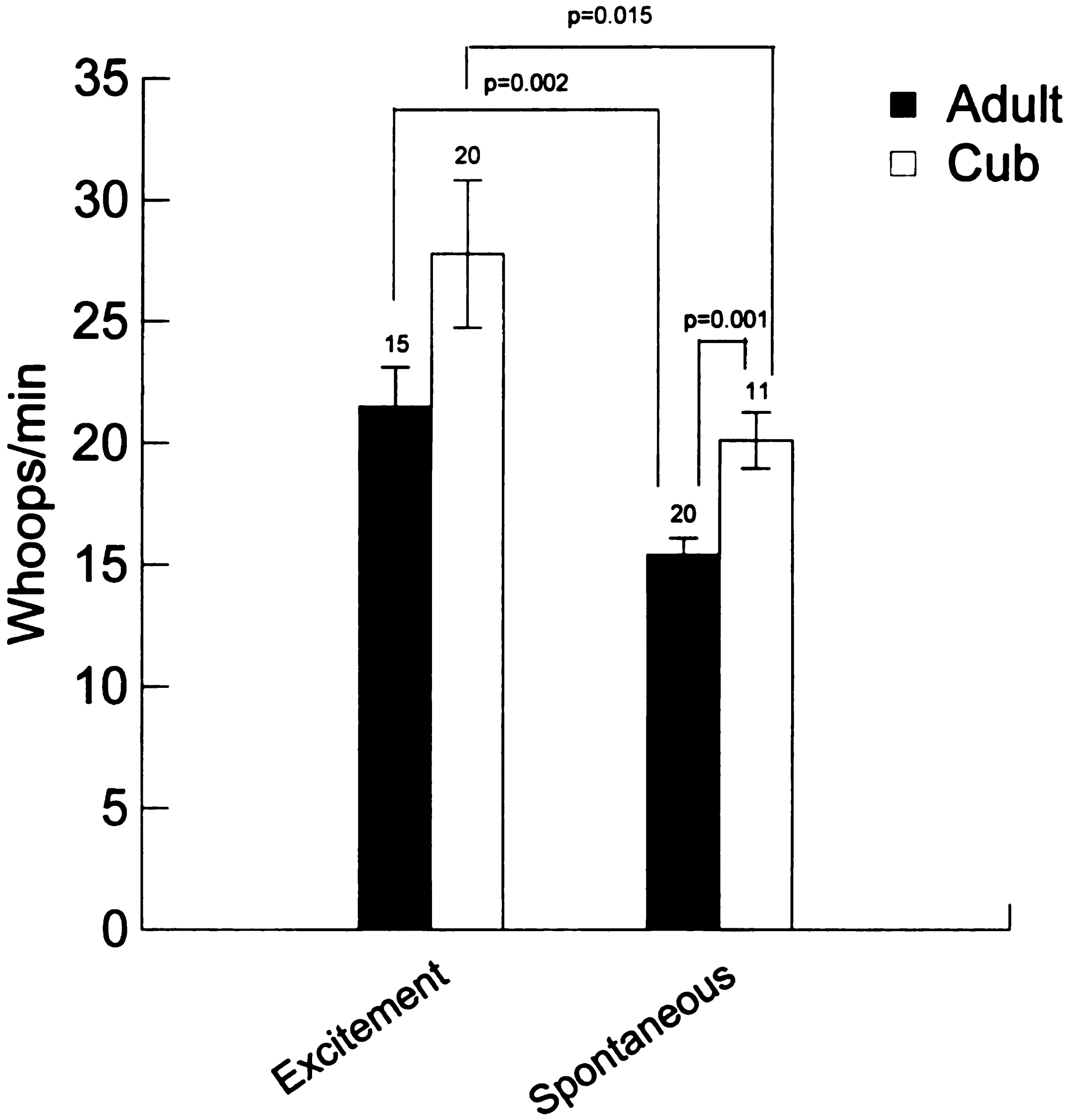


Figure 2.10 Relationship between context and whoop rate (mean ± SE) for adults and cubs. Numbers over bars represent the number of individuals observed in a given context.

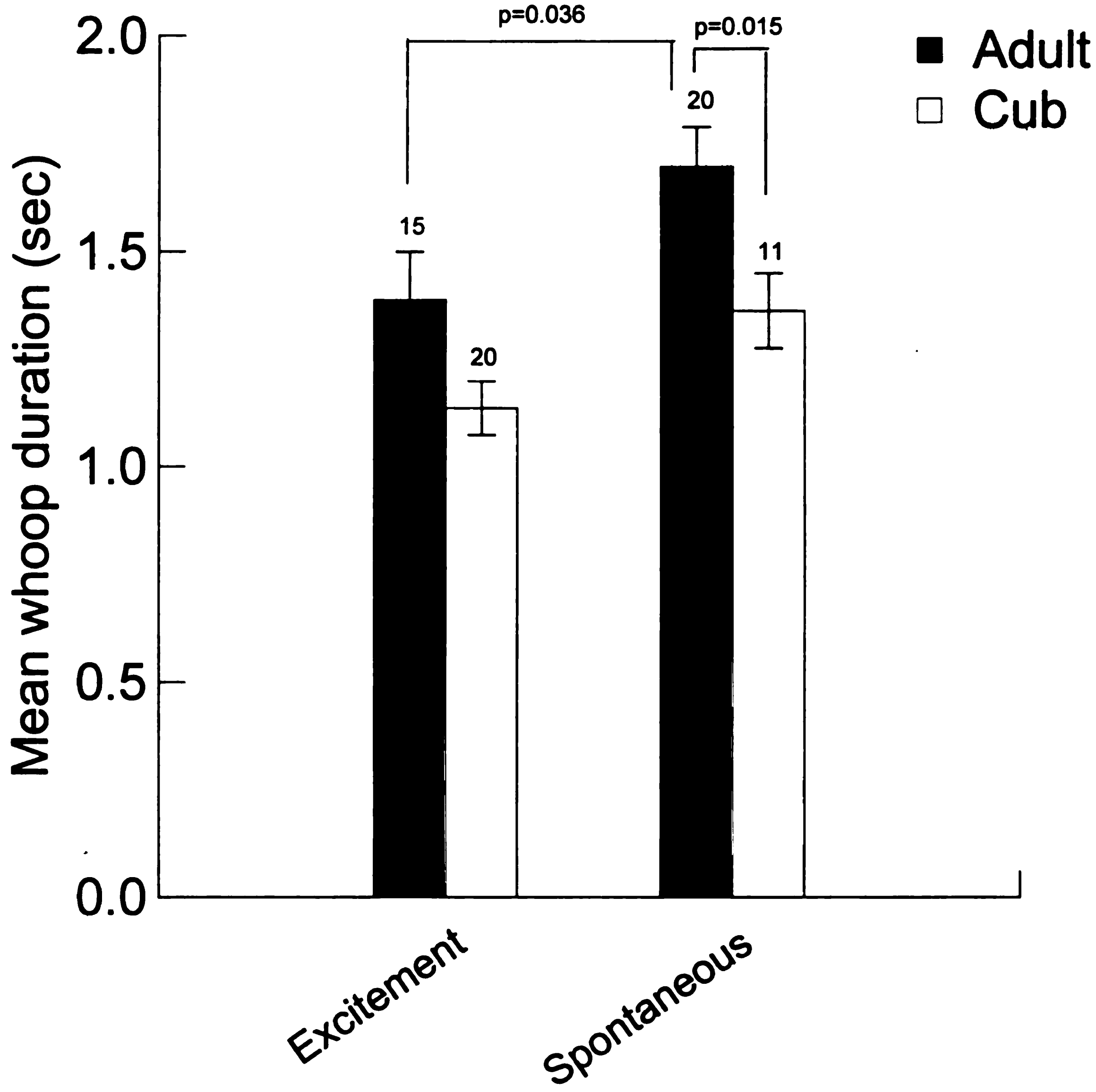


Figure 2.11 Duration (mean ± SE) of individual whoops in bouts produced by adults and cubs in different contexts. Bar labels as in Figure 2.10.

There were also significant effects of both age and context on the duration of inter-whoop intervals within a bout (age: U=745, p=0.009, context: U=225, p<0.0001; Figure 2.12). Although there was an apparent effect of sex on this bout parameter (U=337, p=0.039), there was no effect of sex when controlled for age and context (adults: excitement U=15, p=0.734, spontaneous U=22, p=0.099; cubs: excitement U=36, p=0.452, spontaneous U=3, p=0.066). There was no difference between inter-whoop interval length in adults and cubs during social excitement (U=175, p=0.405), however adults produced significantly longer inter-whoop intervals than did cubs when whooping spontaneously (U=168, p=0.017). While adults produced shorter inter-whoop intervals during social excitement than when whooping spontaneously (U=49, p=0.001), there was no difference between contexts for cubs (U=66, p=0.069).

There was a significant effect of age (U=794, p=0.001) and context (U=368, p=0.025), but no effect of sex (U=535, p=0.985), on the average duration of the entire whoop bout. Bouts produced by adults were significantly longer than bouts produced by cubs both during social excitement (U=208, p=0.053) and when whooping spontaneously (U=158, p=0.048; Figure 2.13). There was no difference in bout duration between contexts for either age group (adults: U=106, p=0.142; cubs: U=86, p=0.322). There were no effects of age, context, or sex on the number of whoops per bout (age: U=572.5, p=0.698; context: U=623, p=0.298; sex: U=635.5, p=0.198).

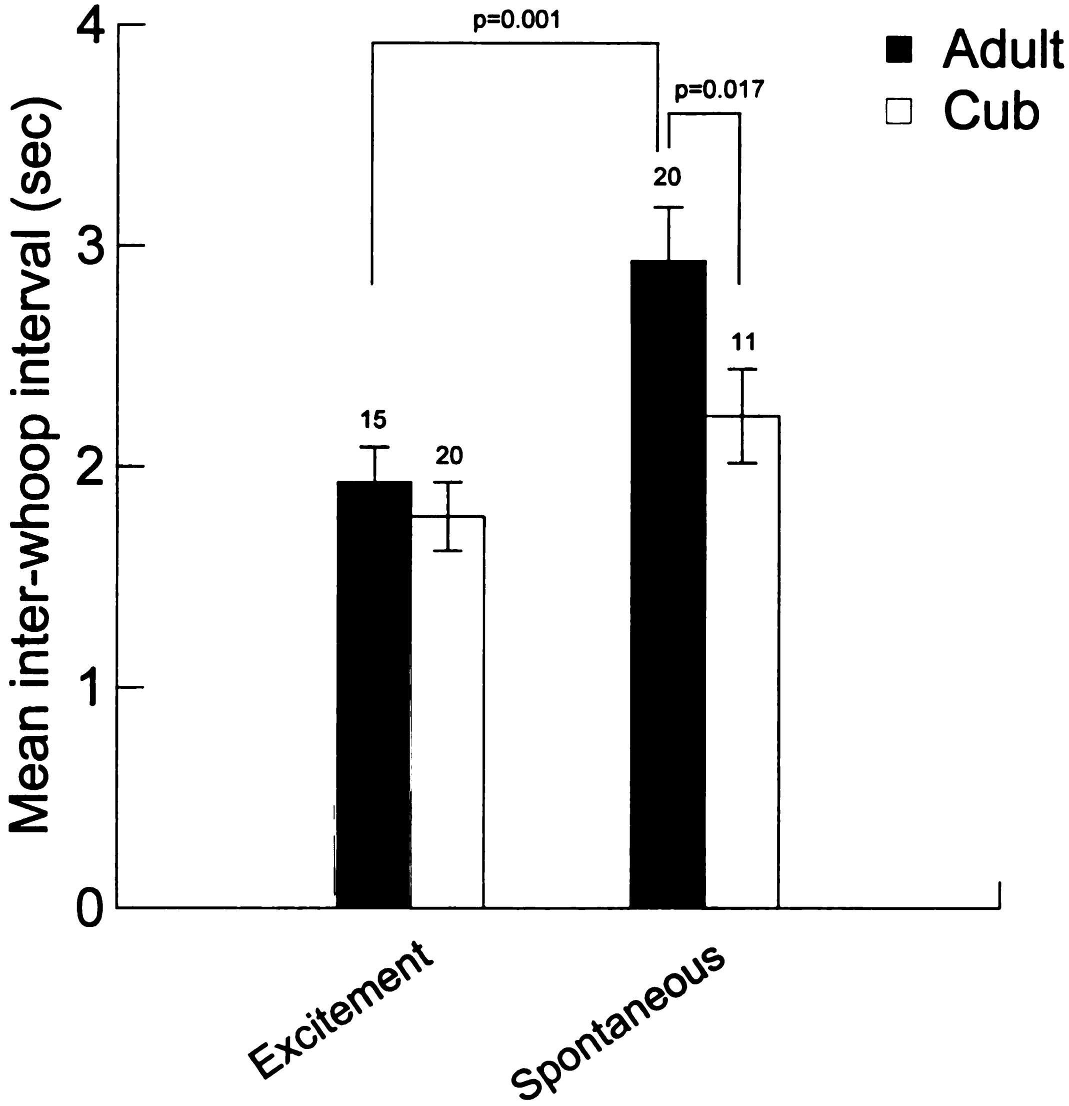


Figure 2.12 Mean (± SE) lengths of inter-whoop intervals in bouts produced by adults and cubs. Bar labels are as in Figure 2.10.

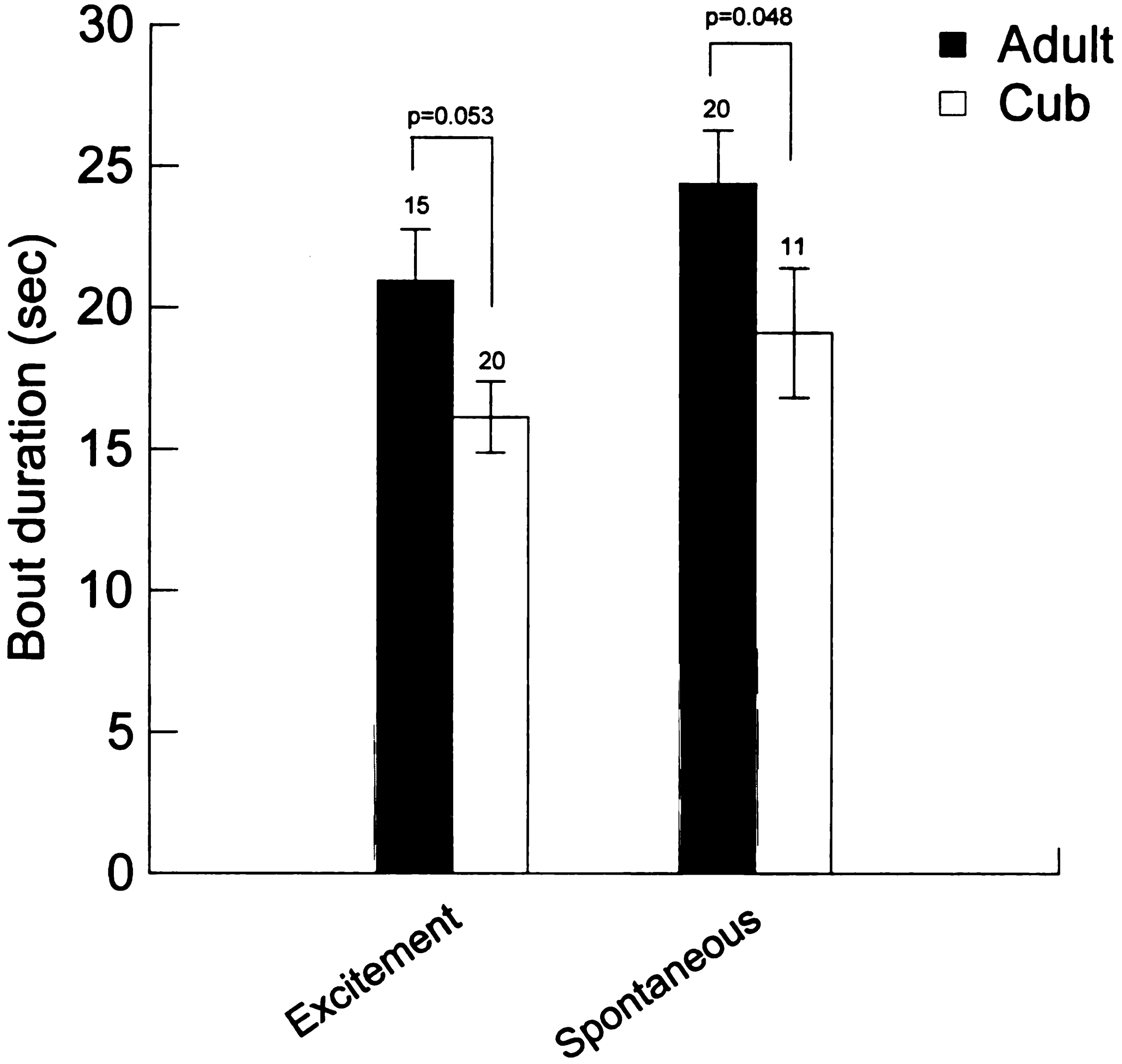


Figure 2.13 Mean (± SE) duration of bouts produced by adults and cubs. Numbers over bars represent the number of individuals emitting whoops in each context.

Responses to whoops

In total, 85 instances from archived data were examined in which we could determine whether or not listeners responded to whoops. We found no difference between the number of arrivals before and after a whoop (Wilcoxon Signed Ranks Z=0.330, p=0.741), however significantly more approaches occurred after the whoop than before (Z=2.953, p=0.003). Therefore, although the arrival of an individual to the scene apparently does not necessarily represent a response to a whoop, the approach of an individual to the caller and/or interaction with the caller was considered here to be a response to the vocalization. For all subsequent analyses we considered a whoop to have received a response only if hyenas approached the caller or the individuals who had been interacting with the caller at the time the whoop occurred.

The reaction to whoops by listening hyenas could be identified for 105 audio recordings. Average values for all 5 acoustic parameters (number of whoops, bout duration, mean inter-whoop interval, mean whoop duration, whoop rate) were calculated when there were multiple whoop bouts emitted by an individual hyena that received the same response. This resulted in 67 cases in which a sound recording was available and the response could be identified. For the following analyses, data concerning context and caller identity from these recorded bouts were combined with data from the 85 archived observations of whooping which were examined previously. Whoops produced spontaneously were less likely to receive a response than were whoops produced during social excitement (n=127, X^2_1=4.547, p=0.033; Figure 2.14). Male and female cubs

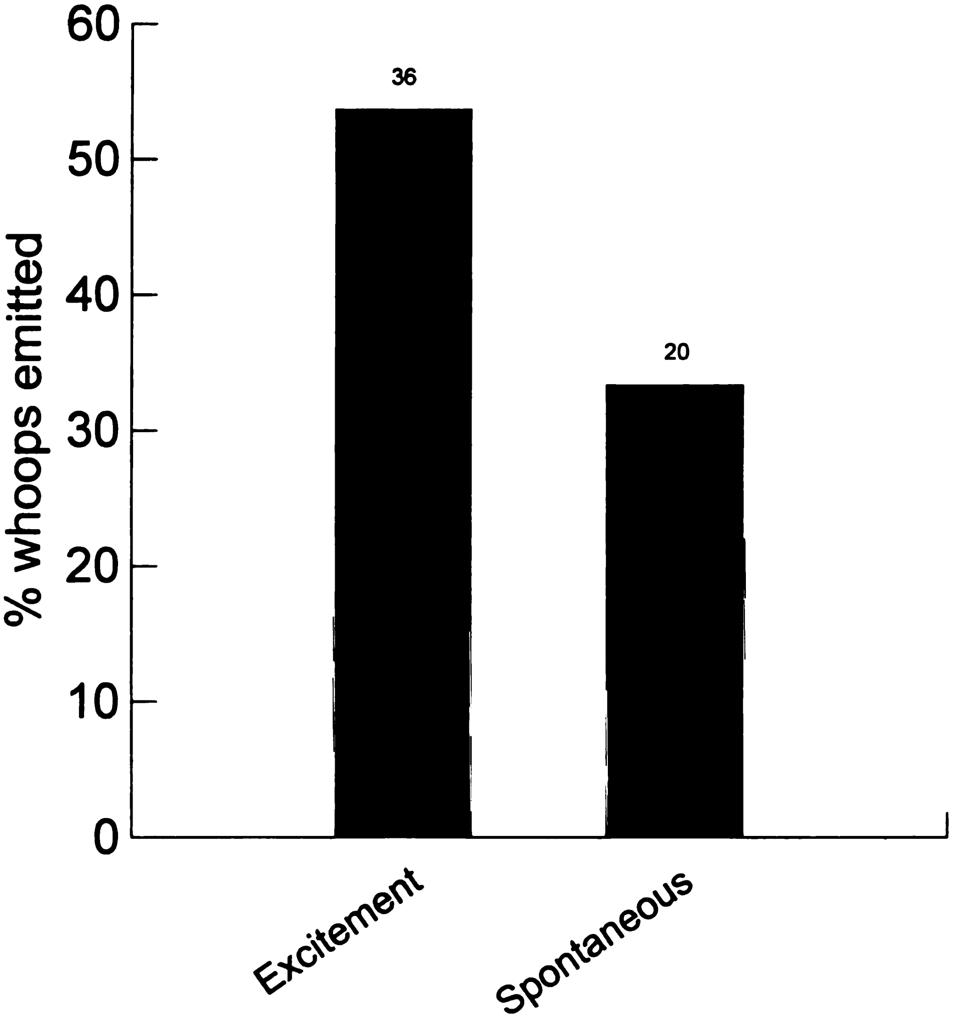


Figure 2.14 Percent of whoops emitted in each context that received a response. Numbers over bars refer to the number of animals receiving a response after whooping in the indicated context.

were equally likely to receive a response (n=88, X^2_1=0.063, p=0.802; Figure 2.15), so these groups were combined in subsequent analyses. Of those instances in which cubs received a response, 37.5% of the responses were by kin (15 responses by kin in 40 cases in which there was a response). Adult females and cubs were equally likely to receive a response (n=115, X^2_1=0.017, p=0.896), although calls by adult females were somewhat more likely to receive a response than were calls by adult males, this difference was not statistically significant (n=64, X^2_1=3.114, p=0.078). However, adult males received responses less often than did cubs (n=125, X^2_1=7.471, p=0.006; Figure 2.15).

Bout parameters and response

For analyses of bout parameters, only calls with both behavioral observations and acoustic recordings were examined. Average values were calculated for any individual with multiple whoop bouts in a particular response category, resulting in 27 cases in which one or more hyenas responded to the caller within 10 minutes of whoop onset, and 40 cases in which no change was observed in the social environment. There was no difference in whoop duration, bout duration, or number of whoops, between calls that received responses and those that did not (whoop length: Mann-Whitney U=492.5, p=0.111; bout duration: U=576, p=0.511; number of whoops: U=751, p=0.188). However, calls that received a response were characterized by higher whoop rates (U=883, p=0.005; Figure 2.16a), and shorter mean inter-whoop intervals (U=311, p<0.0001; Figure 2.16b), than were calls to which no response was observed.

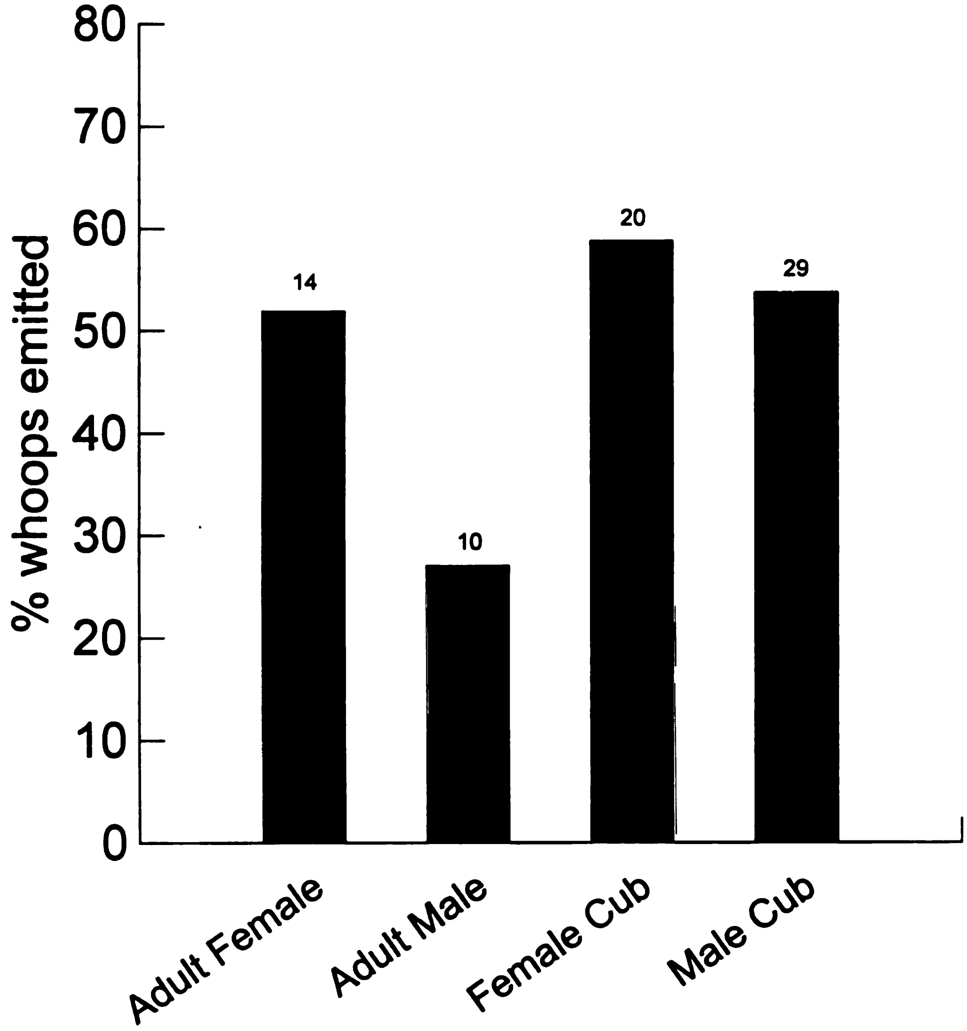


Figure 2.15 Percent of whoops emitted by each sex/age class that received a response. Numbers over bars refer to the number of animals receiving a response.

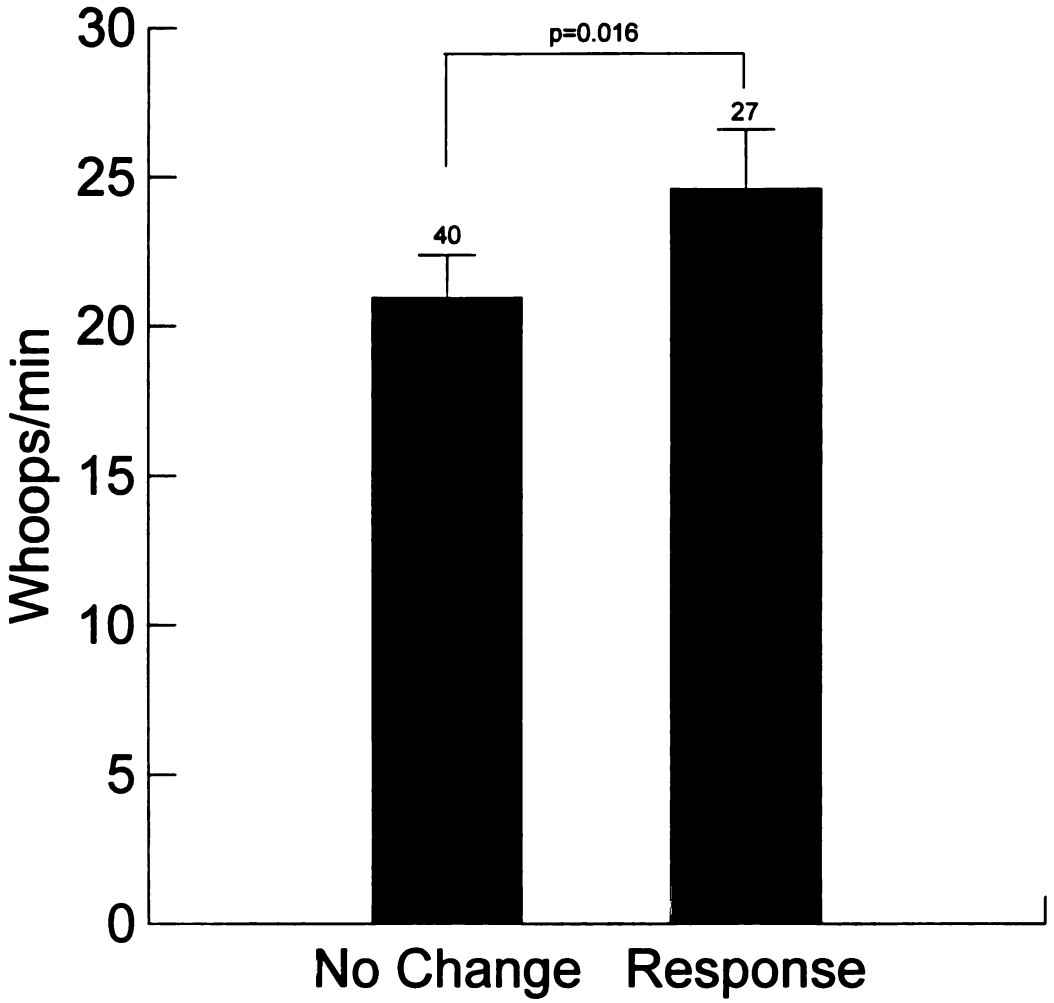


Figure 2.16a Relationship between whoop rate (mean ± SE) and response. Numbers over bars represent the number of individuals receiving the indicated response.

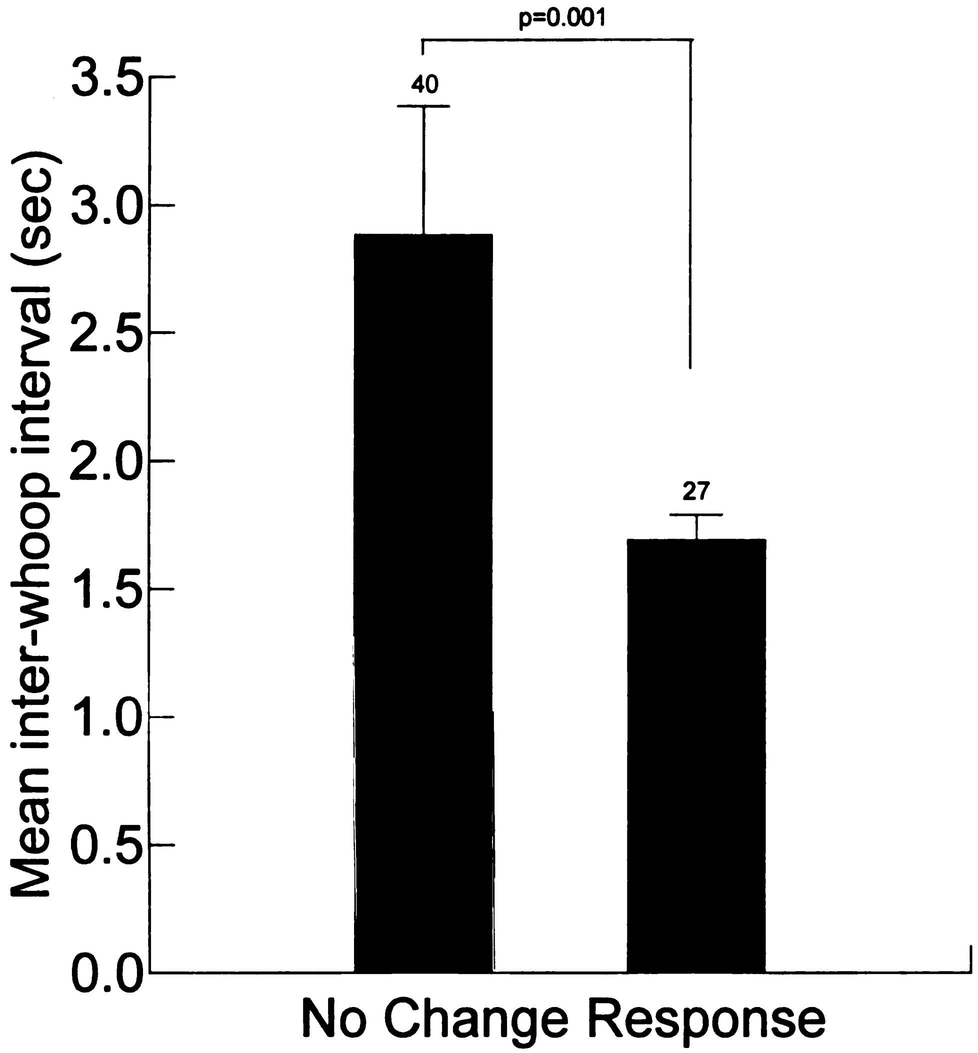


Figure 2.16b Relationship between duration of inter-whoop interval (mean ± SEM) and response. Bar labels as in 2.16a.

Effects of whoop type

All recorded bouts contained either entirely Type A whoops or some combination of Type A and Type S. Type T whoops occurred at the end of 42 of 131 (32.1%) bouts. There was no difference between sex/age groups in the likelihood that a Type T whoop would occur at the end of a bout (n=131, X^2_3= 0.284, p=0.963). There was no effect of context on the likelihood of a bout including a Type T whoop (n=99, X^2_2= 0.005, p= 0.943), nor were bouts containing a Type T whoop more or less likely to receive a response than bouts not containing a Type T whoop (n=103, X^2_1= 0.016, p= 0.901).

Discussion

Previous work by other researchers has shown that acoustic features of spotted hyena whoops vary with age, sex, and individual identity (East & Hofer, 1991a, b; Holekamp et al., 1999). Holekamp et al. (1999) used playback experiments to determine whether spotted hyenas can identify individual conspecifics by their whoops. Mothers were more likely to respond to the calls of their own offspring than to those of unrelated juveniles, and they also gave stronger responses to the calls of younger cubs than to those of older offspring, indicating that whoops contain information about a caller's age in addition to communicating individual identity (see also East & Hofer, 1991a).

East and Hofer (1991a) found that calls produced by cubs typically contained fewer harmonics, wider spacing between harmonics, a higher fundamental frequency, a shorter duration of the low frequency section, and fewer individual whoops per bout than did calls produced by adults. Additionally, these earlier works found that calls given by adult females had lower fundamental frequencies than those given by adult males. Here we replicated their earlier findings that cubs produced whoops with higher fundamental frequencies than adults, and males produced higher fundamental frequencies than did their female peers. We also found that as cubs mature, the fundamental frequencies of their whoops decrease. In most mammals, the fundamental frequency of the call is primarily dependent on morphological factors such as glottal width, vocal cord length, and length of the resonating tube (Michelson, 1983). Ontogenetic changes in these parameters are the most likely sources of frequency variation among calls produced by spotted hyenas, since we found no relation between social context and the fundamental frequency of the whoops. Increased lung capacity and chest girth may also explain the differences we observed in whoop length between cubs and adults. Although East and Hofer (1991a) found Type T whoops more likely to be found in male bouts than female bouts, as well as more likely in adult bouts than in cub bouts, we found no difference between sexes or age classes in the use of this whoop type. Since the composition of bouts does not appear to vary with sex, age, or context, or affect the probability of receiving a response, the functional significance of Type A, S, and T whoops remains unknown.

Here we have demonstrated that sound features vary with the circumstances under which each whoop bout is emitted. Hyenas in the present study whooped in socially interactive contexts, but also whooped for no apparent reason. Both adults and cubs whooped faster when they were stimulated by social excitement than when they whooped spontaneously. Whoops given in these two types of situations most likely have different functions, as indicated by the greater likelihood of receiving a response when whooping during excitement. Hyenas occasionally whooped following greetings, which might simply offer an alternative source of social excitement. The whoop rate may function to alert conspecifics to the caller's internal state, while other acoustic features signal the caller's identity. Although whoop rates did not differ between age groups in contexts involving social excitement, cubs whooped faster than adults when there was no apparent stimulus for their vocalizations. Our results thus indicate that spotted hyenas vary the rate at which they emit whoops according to the circumstances prompting them to vocalize, and they do so by changing both the duration of the individual whoops and the duration of the intervals between them.

As occurs in hyenas, subtle acoustic variations specific to the social context and function of the call are produced by Japanese macaques (*Macaca fuscata*, Green, 1975), cotton top tamarins (*Sanguinus oedipus*, Snowdon et al., 1983), and vervet monkeys (*Cercopithecus aethiops*, Cheney & Seyfarth, 1982; Seyfarth & Cheney, 1984). Common marmoset (*Callithrix jacchus*) 'phee' calls can function to reunite a group, locate mates, or assess the reproductive condition of a prospective mate. Call subtypes specific to these different functions consistently differ in both acoustic frequency and temporal parameters (Norcross & Newman, 1993; Norcross et al., 1999). Some non-primate mammals change features of their alarm calls based on response urgency, as seen in ground squirrels (*Spermophilus beecheyi*, Owings & Virginia, 1978) and marmots (*Marmota flaviventris*, Blumstein & Armitage, 1997). Brant's whistling rats (*Parotomys brantsii*) modify the duration of their alarm calls (Le Roux et al., 2001) and Richardson's ground squirrels (*Spermophilus richardsonii*) vary the rate of alarm calling (Warkentin et al., 2001) based on the degree of perceived threat. Whistling rats produce shorter calls in high-risk than in low-risk situations, while ground squirrels produce a faster call when the predator is closer. Other species vary the acoustic properties of their alarm calls based on the type of predator threat. Aerial and terrestrial predators elicit acoustically different alarm calls, and receive different responses from listeners in chickens (*Gallus domesticus*) (Gyger et al., 1987), vervet monkeys (Seyfarth et al., 1980b), and ring-tailed lemurs (*Lemur catta*) (Macedonia, 1990). Suricates (*Suricata suricatta*) integrate both information about response urgency and predator type into their alarm calls (Manser, 2001). In contrast to the whoop vocalizations of spotted hyenas, alarm calls are typically only given in the presence of a predator, and are usually simple in structure (Bradbury & Vehrencamp, 1998).

Spider monkey (*Ateles geoffroyi*) 'whinny' calls are loud calls with subtypes varying in the frequency dimension (Teixidor & Byrne, 1999). Playbacks of calls recorded in different contexts elicit consistently different responses, but determination of call context by recipients first requires identification of the caller (Teixidor & Byrne, 1999). In this case, calls are context-specific, but individual variation apparently requires listeners to be familiar with the individual vocal signatures of all group members to discern call meaning. It is not yet known what role, if any, familiarity with individual vocal patterns plays in spotted hyena communication.

The context-dependent vocalizations described above are examples of long-distance calls. In short-distance calls emitted by some mammals, acoustic features do not appear to vary with context. Mountain gorilla (*Gorilla gorilla*) double-grunts consist of at least two subtypes differing only in the frequency of the second formant (Seyfarth et al., 1994). For this short-distance call, only the acoustic structure of the double-grunt influences listener response, and the behavioral context in which the call is emitted does not appear to play a role in determining the parameters of the sound (Seyfarth et al., 1994). Acoustically different subtypes also occur in baboon (*Papio cynocephalus*) grunts, but listener's responses vary with context and the caller's identity (Rendall et al., 1999). It may be that the effectiveness of calls functioning to convey information to animals in the caller's immediate vicinity varies with the receivers' perception of the circumstances, whereas calls designed to communicate with distant conspecifics must transmit contextual information to individuals who have no knowledge of the caller's current condition.

East and Hofer (1991b) inquired what prompted hyenas of each age/sex class to whoop while at the communal den, and suggested possible functions for these calls. They observed that most cub whoops occurred either spontaneously (with no apparent preceding stimulus), or when the individual had been attacked or was otherwise agitated. These authors suggested that spontaneous cub whoops function as self-advertisement, but that agitated whoops function to elicit support. They observed adults of both sexes whooping spontaneously more frequently than in any other context. Adults also whooped after being attacked, or after witnessing an attack on another clan member, perhaps to request support or to remind listeners of the whooping animal's identity. Mothers often whooped to call cubs, and adults of both sexes whooped in reply to distant calls, apparently indicating their current location. Adults whooped to recruit conspecific aid during interactions with lions or rival clans, and males sometimes directed whoops at other clan members or whooped while scent-marking, possibly as an inter- or intra- sexual display (East & Hofer, 1991b). East and Hofer (1991b) found that adult males called more frequently than adult females, and that high-ranking adults vocalized at higher rates than did same-sex subordinates.

In the present study, cubs and adult females did not whoop more often in any one context, but adult males most often whooped spontaneously. Since whoops produced spontaneously typically have slower whoop rates, indicating low levels of excitement, whoops produced for no apparent reason probably function to advertise identity and location. Adult males are almost always immigrants (Smale et al., 1993) and therefore might be expected to advertise their identity and presence within the home range more frequently than natal animals. Doing so may signal to females that a male is in the home range at that moment, possibly decreasing the rates of aggression he experiences, or increasing his chances of mating, by familiarizing females with his presence in the home range. Additionally, whooping may announce to prospective immigrants that there is at least one adult male already present in the clan (East & Hofer, 1991b), and in fact may inform listeners about male queue length in the clan (East & Hofer, 2001; Engh et al., 2002).

Both the length of individual whoops and duration of inter-whoop intervals affect the rate at which whoops are produced within a bout. The data presented here did not show dichotomous "slow" and "fast" whoop subtypes as Kruuk (1972) suggested, but rather a range of whoop rates with no distinct group demarcation. Modulation of whoop rate may provide listeners with functionally different whoop subtypes that convey different information. Calls here that received responses generally had higher whoop rates than those that did not. Hyena audiences may be better able to discern the current general state of the caller as indicated by the acoustic properties of the sound, than the specific circumstances under which the call is emitted. Since variations in whoop rate and inter-whoop interval are associated with variations in context, it is not surprising that the response of listeners varies with these cues. Interestingly, cubs were not more likely than adult females to receive responses to their calls. The data presented here also indicate that male and female cubs are equally likely to receive responses to their calls, suggesting that listeners do not discriminate based on the sex of the calling cub.

Variation in conspecific response to acoustic signals has been studied in a variety of social mammals. Chacma baboons produce different bark calls in different contexts, listeners respond differently to bark variations given in high-risk and low-risk contexts, and these calls exist in graded variants (Fischer et al., 2001). Scream subtypes in rhesus monkeys (*Macaca mulatta*) and pigtail macaques (*Macaca nemestrina*) differ with respect to several measures (including bandwidth, number of pulses, and frequency modulation), and conspecifics respond differentially to different scream subtypes (Gouzoules et al., 1984; Gouzoules & Gouzoules, 1989). Fischer (1998) correlated the acoustic structure of Barbary macaque (*Macaca sylvanus*) 'shrill barks' with their eliciting stimuli, and a series of playback experiments determined that receivers perceived two distinct categories of calls. Within each call category, recipient responses were consistent regardless of whether inter-individual differences between calls were small or large. Thus, individual variation within a subtype may not necessarily affect the meaning of the call.

Acoustic features of spotted hyena calls vary with age, sex, and context. Furthermore, particular acoustic features of hyena calls appear to elicit particular types of responses from listeners. Additional research is needed to document the relationship between call structure and different intensities of response. In this study, sample sizes were too small to examine the relationship between call structure and response intensity. Due to the high potential for vocal recognition in this species, field experiments could be used to determine the extent to which recognition occurs. While it is clear that individual recognition occurs in spotted hyenas (Kruuk, 1972; East & Hofer, 1991a, b; Holekamp et al., 1999), the specific acoustic features and mechanisms (genetic relatedness, familiarity, etc.)

mediating individual recognition are still unclear. Similarities between the calls of mother and cub, siblings, or within a matriline, might offer a mechanism for identifying possible allies from a distance. Since spotted hyenas are highly territorial, the existence of acoustic features specific to particular clans could potentially facilitate the identification of alien intruders without the necessity of visual sightings. Hofer et al. (2001) demonstrated that hyenas could identify clan members by scent. Vocal cues might offer yet another method for hyenas to determine the clan affiliation of unseen conspecifics.

Chapter 3

ESTIMATING TERRITORIAL BOUNDARIES OF SPOTTED HYENA CLANS USING PLAYBACKS

Introduction

The use of pre-recorded sounds as a method of attracting animals ("call-ins") has been used to estimate the density of spotted hyena populations (Kruuk, 1972; Creel & Creel, 1996; Mills, 1996; Ogutu & Dublin, 1998; Mills et al., 2001), but has never been applied to determining defended territory boundaries. Traditionally, territorial boundaries have been defined through connecting the outermost points at which individually distinguished hyenas are resighted (i.e. Whateley & Brooks, 1978; Frank, 1986a; Boydston et al., 2001). Conventional techniques rely on long-term, intensive monitoring of multiple individuals per clan, which may be impractical if researchers seek to chart the boundaries of more than one territory, or rapidly determine the number of clans inhabiting a geographical area. This study sought to determine whether established call-in procedures could be used to delineate the boundaries of spotted hyena clans by inciting territorial behaviors, and then connecting the points representing locations where such behaviors have been observed.

Spotted hyenas are gregarious carnivores that defend group territories (Kruuk, 1972; Frank, 1986a). Boundaries are maintained through border patrols in which groups of individuals engage in scent-marking via the deposition of anal gland secretions ('pasting' see Kruuk, 1972; Boydston et al., 2001), as well as establishment of communal "latrines" at which multiple hyenas defecate (Kruuk, 1972). In instances where large groups of hyenas from two neighboring clans are present in territorial boundary areas, clashes, or clan "wars", may occur during which both sides participate in coordinated rushes and attacks and give frequent long-distance vocalizations (whoops) to recruit allies from afar (Kruuk, 1972; East & Hofer, 1991b; Boydston et al., 2001).

Spotted hyenas generally forage within their own territories, hunting medium and large-bodied ungulates, and territorial defense is often associated with competition for food resources (Kruuk, 1972; Henschel & Skinner, 1991). Even in areas of the Serengeti where aliens in transit are tolerated within a territory, commuters who feed on prey outside of their home territories are routinely attacked by resident hyenas (Hofer & East, 1993). Here I hoped to exploit the well-documented aggression directed by hyenas towards intruders to determine where clan territorial boundaries occurred throughout the Masai Mara National Reserve in Kenya. Specifically, I hoped to stimulate such agonistic interactions by attracting hyenas from multiple clans to selected sites using recorded vocalizations.

Methods

Study area and call-in site selection

This study was conducted between May and August 2000 in the Masai Mara National Reserve (MMNR) in southwest Kenya. The MMNR covers approximately 1, 530 km^2 of rolling plains consisting of short and tall grasslands with scattered *Acacia* woodlands, and thickets of *Croton sp.* and *Euclea sp.* Dense forests border the rivers, and multiple seasonal streams crisscross the reserve. Spotted hyenas in MMNR are organized into clans that defend discrete territories (Frank, 1986a; Boydston et al., 2001).

Previous studies have suggested that hyenas are attracted to playbacks from a maximum of 2.5-3.5 km (Mills, 1996; Ogutu & Dublin, 1998; Mills et al., 2001). Using a map of the Reserve, we identified 62 potential call-in sites that were approximately 5km apart. In contrast to Ogutu and Dublin (1998), who used random call-in locations to minimize the effects of territoriality on the numbers of hyenas responding, we sought to exploit the tendency of hyenas to respond in groups (i.e. if one hyena responds, all nearby hyenas will respond). Some locations were chosen to coincide with peripheral areas of hyena clans whose borders had been approximately identified by Boydston et al. (2001), and others were randomly chosen in areas where hyenas have been observed but clan distinctions were not known (Figure 3.1).

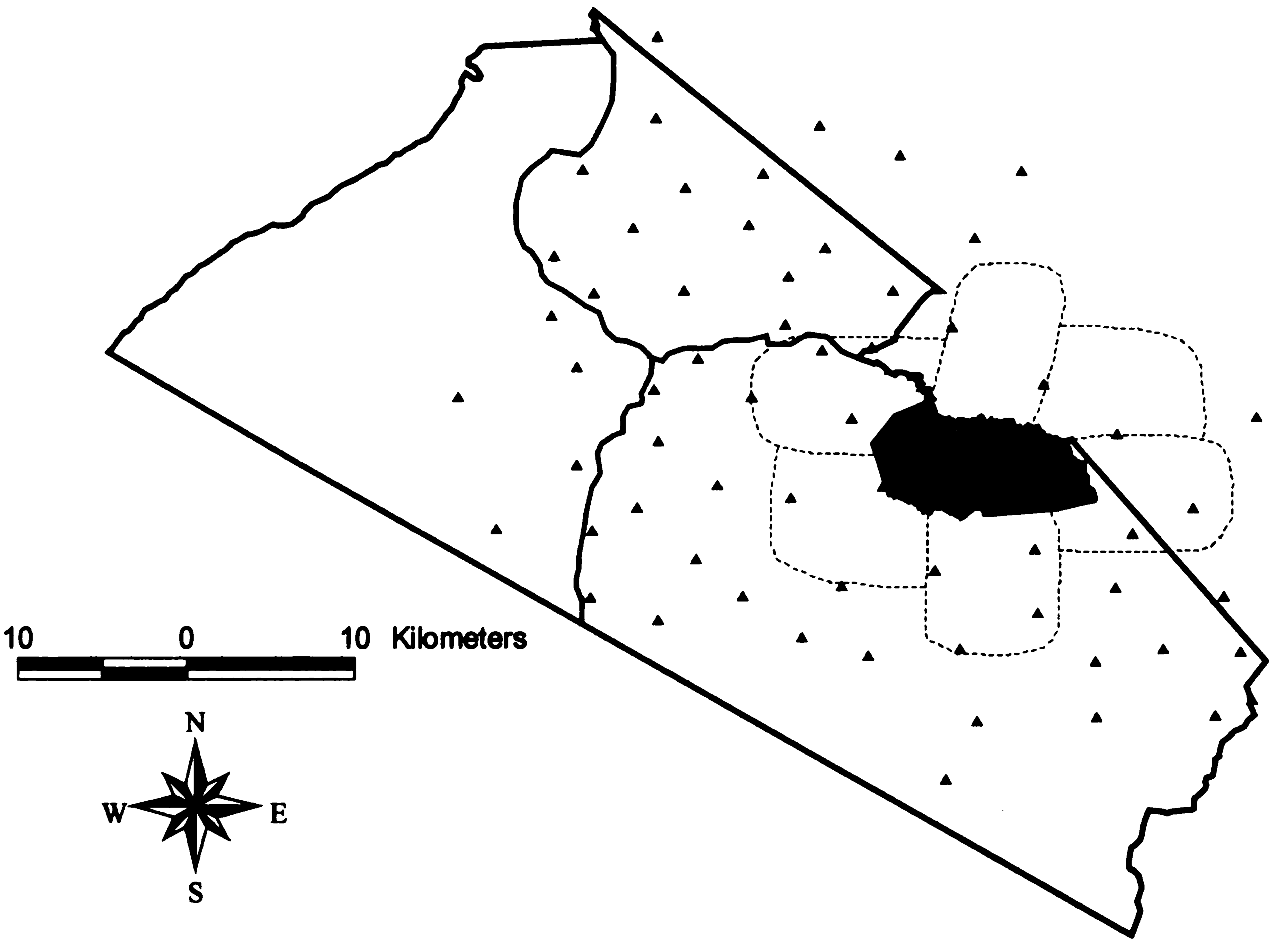


Figure 3.1. Map of the Masai Mara National Reserve showing 62 potential call-in sites. The shaded area represents the Talek clan home range as defined by Boydston (2001). Dotted lines represent the previously approximated boundaries of neighboring clans. After Boydston (2001).

Call-in stimulus and presentation

We prepared four call-in tapes containing sounds known to attract hyenas: vocalizations of hyenas feeding at a kill, calls from hyenas mobbing lions (*Panthera leo*), an inter-clan altercation, and the sounds of a dying ungulate. Each stimulus tape had been recorded in a different location, and only one contained the sounds of MMNR hyenas. This tape was recorded in the Talek clan home range, whose boundaries were defined by Boydston et al. (2001) (see Figure 3.1). No call-ins in the current study were performed inside the Talek clan borders.

Call-in tapes were broadcast for 6 minutes at full volume using a Marantz PMD-22 portable cassette recorder connected to two 20-watt amplified speakers (Optimus model 32-1240, Tandy Corporation) powered by our vehicle's 12-volt battery. The speakers were mounted in the front windows of the vehicle, facing away from one another (Figure 3.2). Previous studies have suggested that any responding hyenas should arrive within 30 minutes of sound onset, and that they should typically respond in groups (Ogutu & Dublin, 1998; Mills et al., 2001). The area around the call-in station was continuously scanned in all directions by multiple observers for 30 minutes after the beginning of the broadcast. We considered any hyena approaching to within 300m of the vehicle to be responding to the call-in. The information recorded at each call-in included: (i) date, time, and location of the call-in; (ii) number of hyenas arriving and the direction of from which each hyena arrived; (iii) latency of hyena arrival relative to

Figure 3.2 Speakers were placed on platforms mounted in the windows of the vehicle. Due to the curvature of the speaker horns, they did not need to be turned to ensure multi-directional sound broadcast . Photo courtesy of Sofia Wahaj.

sound onset; (iv) behaviors of arriving hyenas (i.e. territorial marking, clan war, etc.); (v) maximum visibility in each compass direction.

All call-ins were broadcast between 0600h and 1000h, and only in the absence of rain and high winds to maximize sound transmission (Larom et al., 1997; Bradbury & Vehrencamp, 1998). In order to avoid habituation, call-ins at adjacent locations were performed at least 3 days apart, and with different recordings. All statistical analyses were performed using SYSTAT software (version 8.0, SPSS, Inc.). All means are reported with standard errors. Maps were generated using ArcView GIS software.

Results

In total, we performed 38 call-ins during the study period (Figure 3.3). When played at high volume, some of our tapes produced distorted sounds. Therefore, the two tapes with the best sound quality were used for the majority of call-ins (n=19 and n=14). Hyenas were attracted to 25 of 38 (65.8%) of call-ins (Table 3.1). Of those 25, the mean number of hyenas seen at a site was 7.480 ±1.224, with only 9 (23.7%) attracting 10 or more hyenas, and a maximum of 25. The mean latency to arrival of the first responding hyena was 5.840 ±1.360 minutes from the onset of sound and 85% of all respondents arrived within 20 minutes. Although lions are known to respond to playbacks of hyena

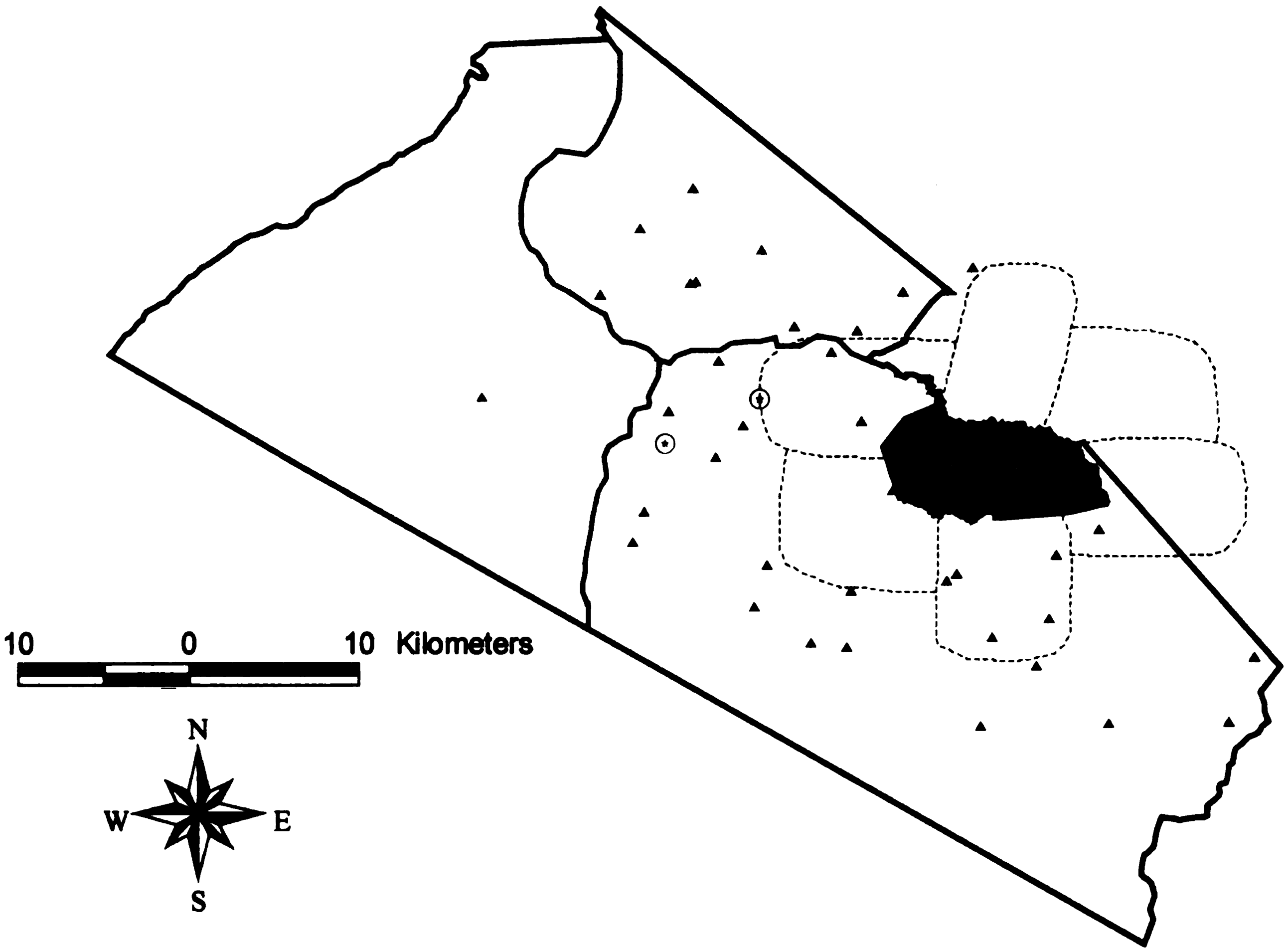


Figure 3.3. Map of Masai Mara National Reserve showing the locations of call-ins performed May-August 2000. Sites represented with stars are locations where territorial behaviors were observed.

Table 3.1 Summary of results from call-ins that attracted hyenas. UTM coordinates refer to the exact geographic location of the vehicle during broadcast. Arrival direction refers to the general compass direction from which we observed hyenas approaching the vehicle.

Call-in	UTM N	UTM E	Date	Total hyenas responding	Latency to first arrival (min)	Mean arrival (min)	Arrival direction(s)
1	9834669	743415	5/19/2000	2	3	6.5	N, NW
2	9829411	746566	5/22/2000	4	3	4.5	SE, NW
3	9839935	735633	5/23/2000	11	0	9.9	N, NW
4	9833456	728859	5/24/2000	2	2	4.5	NW, W
5	9820972	748643	5/26/2000	2	27	27	E
6	9848699	735723	5/27/2000	25	3	7.6	S, W, SW
9	9830913	753072	5/31/2000	14	4	11.2	W, SW
10	9839291	730266	6/2/2000	7	2	6.9	NW, NE
11	9844259	737647	6/5/2000	2	11	16.5	SW, N
13	9828861	740978	6/9/2000	9	7	16.8	SW
14	9842251	733236	6/10/2000	13	1	8.3	E, SW, NW
16	9852273	731704	6/12/2000	3	2	12.3	S, NW
17	9821207	763157	6/13/2000	8	7	18.9	SW, S
18	9846081	726311	6/14/2000	1	3	3	W
19	9840113	719362	6/16/2000	11	1	6	S, SW
20	9837368	730146	6/18/2000	3	3	4.3	S, SE
21	9827300	752593	6/19/2000	14	2	9.9	E, SW
25	9846240	744009	6/24/2000	10	3	16.9	SW, NE
26	9824475	751894	6/26/2000	1	24	24	N
29	9829839	747173	6/29/2000	12	2	10.6	NW
30	9831697	728207	6/30/2000	2	13	13	NW
33	9847670	748136	7/2/2000	6	10	15	S, SE
35	9838495	734683	7/4/2000	1	8	8	SW
37	9846853	731927	7/5/2000	7	2	16.1	N, NW
38	9846708	731546	7/18/2000	17	3	4	N, W

vocalizations, lions were attracted to our sites only once; two lionesses walked past our vehicle, but did not stop. During one call-in, we attracted a jackal (*Canis mesomelas.*) in addition to several hyenas. Although no previous study has reported jackals responding to hyena call-ins, Mills et al. (2001) suggested it might be possible to adapt the call-in method for use with this species.

Description of behaviors

Most hyenas arrived at the call-in site running or loping, those who walked were typically following other individuals. Hyenas would often approach to within 50-100m of the vehicle, and tended to search the area surrounding the vehicle, particularly if the sound was still being broadcast.

On two occasions (Call-ins #3 and #20, Figure 3.3), hyenas exhibited possible territorial behaviors upon arrival. During Call-in #3, seven individuals exhibited excitement on arrival (e.g., tails bristled, ears erect and forward) and began pasting as a group. The group then moved off to the south, still bristle-tailed, in what appeared to be a border patrol. Behaviors exhibited during Call-in #20 were less clear: one adult arrived within two minutes of sound onset, and two minutes later additional adults (n=2) ran in from the opposite direction. The second group was bristle-tailed and chased the first hyena for a short distance, then loped away in the direction from which they arrived. Since the number of individuals involved was so small, it is difficult to determine whether the first hyena was an intruder, or simply subordinate to the others.

On all other occasions, responding hyenas exhibited non-territorial behaviors once they arrived at the site. That is, they engaged in greetings, aggressive, and affiliative behaviors associated with intraclan interactions, or simply rested. Hyenas who arrived as a group typically also left the site as a group, and often hyenas departed within 10 minutes of arrival. Here playbacks never elicited a clan war.

Discussion

Two of the recordings used in this study appear to be as effective at attracting hyenas as those used by other studies (Table 3.2), but although Ogutu and Dublin (1998) reported that their call-ins incited clan wars in MMNR, we were unable to stimulate inter-clan interactions. Similarly, Whateley and Brooks (1978) were unable to observe clan wars at any of their call-in stations in Hluhluwe Game Reserve in South Africa, even those on known clan boundaries. While it may be possible to do so, current call-in procedures do not appear to be an effective method of reliably eliciting clan wars.

The combination of sounds used here for call-ins is thought to be effective because the sounds of a kill attract hyenas who are hungry and the sounds of encroaching alien hyenas attract residents even when sated, thus potentially attracting all hyenas within range of the sound. Lions are able to

Table 3.2 Summary of results from studies using playbacks to attract spotted hyenas. The present study represents the only attempt to date to use call-ins to map home ranges; all others used playbacks to census populations.

	Location	Number of Call-ins	Call-ins with Hyena Response	Mean Hyenas per Successful Call-in	Clan Wars Observed
Present Study	Masai Mara National Reserve, Kenya	38	65.8%	7.5	NO
Mills et al. (2001)	Kruger National Park, South Africa	346	65.6%	4.1	n/a
Ogutu and Dublin (1998)	Masai Mara National Reserve, Kenya	192	n/a	10.7 **	YES
Whately and Brooks (1978)	Hluhluwe Game Reserve, South Africa	105	83%	3.4	NO

** Mean approximated from total hyenas observed and the number of call-ins performed. The number of successful call-ins versus those to which there was no response was not reported. After Ogutu and Dublin (1998).

assess group size based on acoustic signals (McComb et al., 1994), but it is unknown whether hyenas can make this distinction. Spotted hyenas may not respond to a call-in if they judge their own social group to be smaller than the perceived size of the intruders' group. To date, no study has examined the ability of hyenas to discriminate between the sounds of clan members and alien hyenas, although this has been demonstrated in other species (lions, McComb et al., 1993; Mexican jays, *Aphelocoma ultramarina*, Hopp et al., 2001). If vocal recognition at this level does not occur, hyenas may be responding only to the sounds of group activity. Spotted hyena societies are characterized by rigid linear dominance hierarchies (Frank, 1986b; Smale et al., 1993; Holekamp & Smale, 1998) in which high-ranking animals typically have more maternal relatives, and hence more potential allies than do low-ranking individuals (Frank et al., 1995; Holekamp et al., 1996). Boydston (2001) determined that low-ranking females spent much of their time near the edges of the territory, while high-ranking females were more often located in the central core area. Therefore, call-ins near a territorial border may be more likely to reach low-ranking individuals who might be most reluctant to approach the sounds of a large group.

Social structure and social behaviors must be considered when examining the results of call-in studies. While call-ins may be an effective, low-cost method of estimating the size of spotted hyena populations, more research is needed before these procedures can be used to map territory boundaries. Rather than attempting to incite clan wars or other territorial behaviors, call-ins could be used in conjunction with mark-resighting or radio-tracking to increase the probability of locating known individuals. Traditional methods of determining territorial borders could then be applied to the resulting set of locations.

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