Sources of variation in the long-distance vocalizations of spotted hyenas

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Summary

It has long been recognized that vocal signals communicate information about the age, sex and affective state of callers. However, the mechanisms by which these types of information are communicated are less well understood. Here we investigated variation in the acoustic properties of the long-distance vocalizations, called 'whoops', emitted by free-living spotted hyenas, *Crocuta crocuta*. Specifically we investigated whether the fundamental frequency, length and rate of whoops provide information about the caller's age, sex and/or level of arousal. We determined the latter by contrasting whoops emitted spontaneously with whoops emitted during periods of social excitement, when callers typically also exhibited visual signals associated with heightened arousal. We found that the minimum fundamental frequency of a whoop provides reliable information about the caller's general age and, for adult callers, information about sex as well. The vast majority of adult male whoop bouts were emitted spontaneously, but juveniles and adult females produced many of their bouts during periods of social excitement. Although context did not significantly affect the whoop bouts of adult females, juvenile bouts emitted during social excitement had higher maximum fundamental frequencies, greater proportions of asymmetric whoop subtypes, and reduced inter-whoop intervals. By reducing the inter-whoop intervals of bouts, juvenile hyenas significantly increased the likelihood that conspecifics would respond to whoops by approaching the caller or its social companion. Peak fundamental frequency and the relative abundance of whoop subtypes did not appreciably affect response. We discuss the potential functions of whooping by juvenile and adult hyenas in light of these findings.

Keywords: *Crocuta crocuta*, fission-fusion, vocal communication, afferent signaling, arousal.

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; Manser et al., 2001; Weiss et al., 2001; Slocombe & Zuberbuhler, 2005b). Responses to vocalizations produced by many species of nonhuman primates vary with call subtype, suggesting that the information communicated in these calls might vary with their acoustic structure (Seyfarth et al., 1980; Cheney & Seyfarth, 1982; Fischer, 1998; Fichtel & Hammerschmidt, 2002; Kitchen et al., 2003; Wich et al., 2003; Slocombe & Zuberbuhler, 2005b). In some species, the structure of particular calls varies predictably with the context in which the calls are emitted (Norcross & Newman, 1993; Rendall et al., 1999; Crockford & Boesch, 2003; Wich et al., 2003; Slocombe & Zuberbuhler, 2005a,b). 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; Papaeliou et al., 2002; Crockford & Boesch, 2003; Notman & Rendall, 2005; Slocombe & Zuberbuhler, 2005a; Patel & Owren, 2007), relatively little research of this nature has been done on other animals (but see Leger et al., 1979; Insley, 1992; Brown & Farabaugh, 1997; McCowan & Reiss, 2001; Pongracz et al., 2005).

The acoustic structure of mammalian loud calls may vary with individual identity, with the caller's age, sex, social status, reproductive and affective state, as well as with particular features of the caller's environment (Marler et al., 1992; Seyfarth & Cheney, 2003). Although it has long been recognized that vocalizations provide information about a caller's affective state (Darwin, 1872; Morton, 1977; August & Anderson, 1987), the mechanisms by which this is indicated remain poorly understood (Fichtel & Hammerschmidt, 2002). Several recent studies have shown that the acoustic structure of mammalian loud calls reflects the caller's level of arousal (Fischer et al., 2002; Rendall, 2003; Wich et al., 2003; Notman & Rendall, 2005). Intensity of arousal, associated with either excitement or fear, might be communicated in vocal signals by elevated pitch, amplitude, or by altered patterns of calling in space and time (Smith et al., 1977; Seyfarth et al., 1980; Fichtel et al., 2001; Manser, 2001; Fichtel & Hammerschmidt, 2002; Fischer et al., 2002;

Bachorowski & Owren, 2003; Rendall, 2003; Wich et al., 2003). The present study documents variation in acoustic structure in relation to caller traits, and investigates the role of call context, in the long-distance vocalization of a gregarious carnivore, the spotted hyena, *Crocuta crocuta*.

Spotted hyenas live in large social groups, called clans, containing several adult, immigrant males and multiple natal, breeding females clustered in hierarchically-ordered matrilines (Kruuk, 1972; Frank, 1986; Mills, 1990). As such, they more closely resemble the societies of many Old World primates than those of other gregarious carnivores (Ewer, 1973; Holekamp et al., 2000). The hierarchical arrangement of *Crocuta* clans is linear and rigid, with immigrant males ranking lower than adult females or their offspring (Kruuk, 1972; Tilson & Hamilton, 1984; Frank, 1986). Female *Crocuta* are also slightly larger than males. Since hyena clans are fission-fusion societies, a rich vocal communication system may facilitate the maintenance of social bonds between clanmates who are sometimes in close proximity to one another, but otherwise separated by long distances (Kruuk, 1972; Ramos-Fernandez, 2005). The whoop vocalization of spotted hyenas is a series of discrete calls produced in a bout of sound that can travel distances of five kilometers or more (Kruuk, 1972). Although Kruuk (1972) was unable to perform formal analyses of the acoustic structure of hyena vocalizations, he perceived two general categories of whoop bouts, 'slow' and 'fast'. Slow whoop bouts constitute a series of 6-9 distinct calls, each lasting 2-3 s, with inter-whoop intervals of 2-10 s. Hyenas typically emit slow whoops while walking, standing or lying down. Kruuk (1972) labeled these bouts 'spontaneous', and several studies have reported that spontaneous whooping is very common (Kruuk, 1972; Mills, 1990; East & Hofer, 1991b). Kruuk (1972) further suggested that fast whoops are characterized by higher pitch, shorter call duration, and shorter inter-whoop intervals than slow whoops, and that they occur during moments of heightened arousal, such as during confrontations with lions or conspecifics.

East & Hofer (1991a) provided the first technical description of *Crocuta*'s whoop, documenting its acoustic structure, individual variation among clanmates, and ontogenetic changes in whoop structure within individuals. They identified three distinct types of whoops, designated asymmetrical (A), symmetrical (S) and terminal (T) (Figure 1). Type A whoops contain an initial
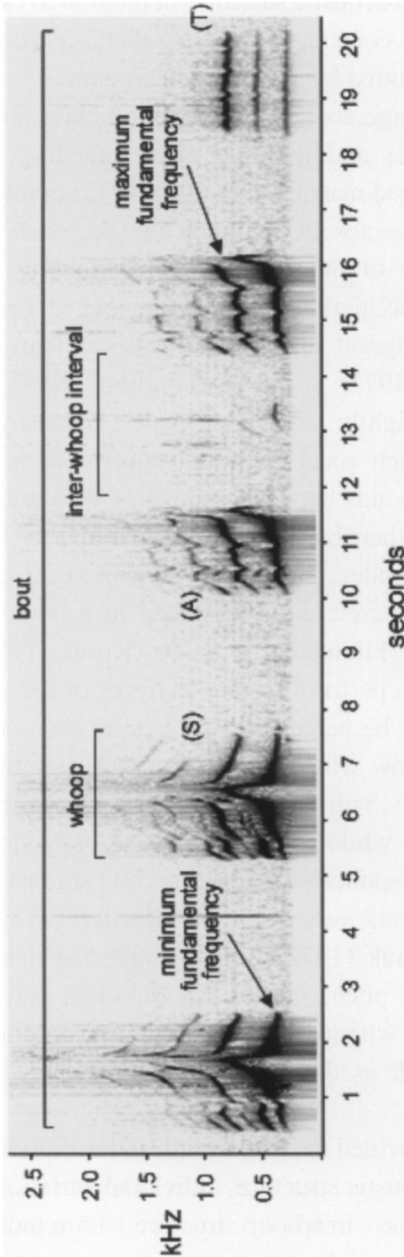
Figure 1. Spectrogram of a spotted hyena whoop bout showing five of the measures obtained. The durations of all discrete calls and inter-whoop intervals were measured and averaged to provide mean values for a bout. Maximum and minimum frequency measures were also obtained from all available calls and an average measure per bout was obtained for each. S, A and T represent examples of symmetric, asymmetric and terminal whoop subtypes, respectively.

low frequency section followed by an abrupt rise. Type S whoops begin with a low frequency section, rise in pitch, and then return to the initial low frequency. Type T whoops are lowing sounds (similar to the monotonous moo of cattle) characterized by little change in frequency, and are typically found at the end of a bout. East & Hofer (1991a) found that male and female spotted hyenas of all ages produced all three whoop types, and bouts typically contained combinations of A, S and T whoops. Observing that type A whoops have shorter call durations and inter-call intervals than do type S whoops, East & Hofer (1991a,b) hypothesized that hyenas could potentially utilize type A whoops to communicate urgency to clanmates during inter- and/or intraspecific agonistic contests, and thereby elicit support. One objective of our study was to test predictions of this hypothesis.

If the acoustic structure of whoops communicates to listeners what is happening to the caller, then the sound produced ought to vary with the circumstances under which the vocalization is emitted. Furthermore, variation in the acoustic structure of whoops should be associated with predictable variation in the responses of listening hyenas. 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 (East & Hofer, 1991a). However, since the basic acoustic structure of the call remains stable within individuals over time, spotted hyenas attending to acoustic signals may be able to use other 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, 1991b). Specifically, the rate at which whoops are produced, and variation in fundamental frequency, may reflect the caller's affective state (Kruuk, 1972; Morton, 1977; Fichtel & Hammerschmidt, 2002).

Although East & Hofer (1991b) described the situations in which hyenas whoop, as well as the average composition of whoop bouts for each age and sex class, they did not address questions about how acoustic variation in the vocalization relates to the caller's traits or circumstances. The present study inquires whether the caller's age, sex, and immediate circumstances influence the acoustic structure of whoops within a bout as suggested by Kruuk (1972), and whether the responses of conspecifics vary with the structure of whoops.

Methods

Study animals

This study was conducted in the Talek region of the Masai Mara National Reserve, Kenya, an area of rolling grassland grazed year-round by moderate to large concentrations of ungulates. The subject population was one large *Crocuta* clan inhabiting a home range of approximately 65 km^2 (Frank, 1986; Boydston et al., 2001). Members of the Talek clan were identified by their unique spot patterns and other conspicuous characteristics such as ear notches. Sex 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 ($\pm$7 days) when first observed above ground at natal or communal dens, based on their pelage, size and other attributes. In this study, hyenas were considered juveniles until they were 24 months of age, and older animals were classified as adults.

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 1989 and 2001. Observers were present in the study area at least 23 days per month, except during April 1991, when observers were present on 14 days. Observations were made at natal and communal dens, at ungulate kills, and away from both dens and kills (e.g., when hyenas were traveling or resting). All occurrences of agonistic interactions, whoop bouts, and arrivals or departures of hyenas were recorded as critical incidents (Altmann, 1974). Additionally, body measurement data were obtained from hyenas anaesthetized with Telazol (W.A. Butler, Brighton, MI, USA; 6.5 mg/kg), delivered from a CO_2-powered darting rifle (Telinject, Saugus, CA, USA). In this study we used chest girth as an indicator of general body size. Estimated ages of adult immigrant males were determined from patterns of tooth wear using methods described in Van Horn et al. (2003).

Whoop contexts

From 1989 to 1998, field researchers studying the Talek clan recorded 117 whoop bouts during routine observation sessions using a Marantz PMD-22 portable cassette recorder and a Sennheiser ME66 directional microphone. For each recorded bout, we noted caller identity, date, time, location and maximum sound pressure. The resulting sound library consisted of whoop

recordings produced by hyenas of all age classes, at locations throughout the Talek range. Information from an additional 82 whoop bouts that had not been tape-recorded was gathered from archived field observations made between 1995 and 2001. For 181 of the 199 total bouts, detailed behavioral observations were available describing the events occurring 10 min before and after each bout. Bouts were excluded from analyses if whoop vocalizations from the focal or any other individual occurred during either of these 10-min intervals.

Following Kruuk (1972), we classified whoop bouts as either spontaneous or occurring during periods of general excitement. Hyenas were often observed whooping spontaneously when there was no apparent stimulus eliciting the call (90/181). 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 spontaneously when approaching or leaving a group of conspecifics in which no social excitement whatsoever appeared to be occurring. In contrast, other whoops occurred when the caller was exhibiting postural cues indicating a high level of arousal, such as holding its head elevated, ears forward, and tail erect and bristled (76/181). Such situations included instances when the caller behaved aggressively toward another individual, when the caller had just been attacked by a conspecific, when the caller was a bystander to aggression directed toward a third hyena, and when the caller was involved in a confrontation with lions or members of a neighboring clan. A third context we initially considered occurred when whoops were emitted following greetings between conspecifics (Mills, 1990). Spotted hyenas often engage in distinctive greeting behavior when they encounter clanmates from which they have been separated (Kruuk, 1972; East et al., 1993). Upon meeting, two hyenas stand head-to-tail, lift the rear leg closest to the other hyena, and sniff one another's ano-genital region. We excluded whoops following greetings from analyses involving context because whoops occurring after greetings were relatively rare (15/181), and because the level of arousal associated with greeting may be substantially different for the two parties involved, depending upon age and social rank. Consequently, we analyzed 166 whoop bouts from 79 hyenas (2.1 ± 0.2 bouts per individual) to determine whether the probability of whooping spontaneously or during social excitement varied with the age/sex class of the caller. Although this involved some pseudoreplication, the patterns were robust and remained even when we compared the proportion of whoops emitted spontaneously by each individual hyena.

Conspecific responses to whoops

Although all hyenas within 5 km of the caller were likely within the range of sound produced during any given whoop bout (Kruuk, 1972; East & Hofer, 1991a), we could only observe events in the immediate vicinity of the caller. Events observed during the 10 min following a whoop 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 conspecific. All of the following were considered to be reactions to a whoop vocalization: an approach to within 1 m of the caller, a social interaction with the caller or another individual with which the caller had been interacting at the time of the whoop, or the arrival on the scene of hyenas not originally present. To avoid ambiguity, a mere change in body or head orientation in relation to the caller was not considered to be a significant response. We were able to determine unambiguously whether or not 174 of the 181 bouts elicited responses from conspecifics.

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-Sonagraph Pro software package (version 2.7, Raimund Specht, 2000, Berlin, Germany), with a Hamming window and a Fast Fourier Transformation length of 512. From each recorded bout we extracted the following acoustic measures: total bout duration, number of whoops per bout, the duration of each whoop within the bout, the duration of each inter-whoop interval, and the minimum and maximum fundamental frequencies of each call (Figure 1). Bout duration was defined as the time elapsed between the beginning of the first whoop 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, and each call was identified as being an A, S or T whoop. Whoop duration was measured for all available calls within the bout, and inter-whoop interval was determined by measuring the time elapsed between the end of each call in a bout and the beginning of the next call. Since the acoustic frequency of whoops varies over the duration of the call, and because each whoop type (A, S, T) has an inherently different pattern of frequency change, we used minimum and maximum fundamental frequencies to represent the

vocal pitch of whoops. The fundamental frequencies of each call were obtained through visual inspection of the spectrograms (Peters et al., 2004), and averaged within a bout. For one analysis, regarding whether hyenas varied the minimum and peak fundamental frequencies of bouts with context, we used the Syrinx sound analysis program (same specifications as above; version 2.6h, John Burt, www.syrinxpc.com). Finally, 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.

The 117 recorded whoop bouts were obtained from 60 different hyenas (15 juvenile females, 13 juvenile males, 17 adult females and 15 adult males). In assessing age and sex-related variability in minimum fundamental frequency, we avoided pseudoreplication by randomly selecting a single digitized bout from each hyena. In analyses of the effect of age/sex class on acoustic parameters other than fundamental frequency, if multiple bouts had been recorded for an individual within a particular age class, then averages were calculated for each acoustic measure (whoop rate (rate), mean whoop duration (duration), mean inter-whoop interval (interval), bout length (length) and mean number of whoops per bout (number)). This yielded measures for sixty hyenas (1.95 ± 1.7 bouts per hyena; range: 1-11). Two recorded bouts containing only a single whoop were excluded from analyses of inter-whoop interval and whoop rate.

In analyzing the effects of context on the acoustic parameters of whoop vocalizations, individual hyenas were used to represent only one contextual category. When multiple bouts were available for an individual in a single context, mean values were calculated for each acoustic parameter. This yielded 53 cases with known context and bout parameter values. Of the fifteen adult males from which we obtained audio recordings, only two whooped during social excitement. Therefore, we were unable to analyze the effect of context on the acoustic parameters of adult male whoop bouts.

To determine the effects of bout parameters on the likelihood of listener response, we calculated average parameter values for each individual hyena from all whoops eliciting an unambiguous response, and from all whoops that did not elicit a response. If a hyena was represented in both categories ($N_{af} = 1/14$, $N_{juv} = 5/21$), we randomly selected which they would represent in the analysis. Adult males were excluded from this analysis as they

seldom received responses to their whoops (9/49 bouts, with one male accounting for 5/9 bouts receiving a response). Juveniles and adult females were analyzed separately because the acoustic parameters of their whoop bouts differ significantly (see below). For adult females, we analyzed 7 cases in which one or more hyenas responded to a whoop bout, and 7 cases in which no significant change was observed in the social environment. For juveniles, we analyzed 10 cases in which an unambiguous response was evident, and 11 cases in which no response was observed. Multiple logistic regression models were constructed for adult females and juveniles that included peak fundamental frequency, bout length, number of whoops in a bout, whoop rate, inter-whoop interval, and mean call duration as independent variables, with response as the dependent variable.

Statistical analyses

Relationships between minimum fundamental frequency, chest girth and age were evaluated using piecewise linear regression (STATISTICA, version 6.1, 2002, Quasi-Newton Method), and nonlinear curve fitting (GrowChoice, H.D. Sheets, 2003, Buffalo, NY, USA). Alternative models were evaluated using the serial autocorrelations (AC) among residuals, percent variance explained and the Akaike information criterion (AIC) estimates (Zelditch et al., 2003). The effects of call duration and inter-whoop interval on whoop rate were determined by linear regression analyses of natural log transformed data. The bout parameter data were not distributed normally and therefore were analyzed using chi-square, Wilcoxon matched pairs, Kruskal-Wallis and Mann-Whitney U-tests. The absence of sufficient repeated measures for individual hyenas precluded our performing discriminant function analyses. We used logistic regression to assess the effects of social context, acoustic parameters, and the relative abundance of type A whoops in bouts on the likelihood of conspecific response (SAS, version 8.02, 2001, stepwise selection method; Karp, 2000; Pampel, 2000). Mean values are presented $\pm$ standard error. Statistical significance in tests involving multiple comparisons was evaluated using the Holm's sequentially-rejective Bonferroni method (Shaffer, 1995). Other differences between groups were considered statistically significant when $p < 0.05$. All statistical tests were two-tailed.

Results

Effects of age and sex on bout parameters

The minimum fundamental frequencies of whoop bouts ranged from 583 Hz in a 4-month-old cub to 219 Hz in a 104-month-old adult female ($N = 60$; Figure 2a). As hyenas mature, their voices deepen steadily until late in the third year of life. Ontogenetic variation in minimum fundamental frequency revealed a pattern similar to that for chest girth ($N = 251$; Figure 2a,b), suggesting that body size might influence vocal pitch. In both sexes, the development of chest girth and minimum fundamental frequency strongly conformed to the German Gompertz model for biological growth (Fiorello & German, 1997; Zelditch et al., 2003; Table 1). The asymptote of the model for male minimum fundamental frequency was greater than the respective asymptote for females, and the asymptote for chest girth among males was less than that among females. Piecewise linear regression analyses revealed that the rates of development of both minimum fundamental frequency and chest girth changed most significantly at 12-16 months of age in hyenas of both sexes (Table 2). However, as in our nonlinear curve fitting analyses, the breakpoint for fundamental frequency was greater for males than females, while the breakpoint for chest girth was greater in females than males.

Among adults, the whoop bouts of females were characterized by lower minimum fundamental frequencies than those of males (Mann-Whitney U test; $U = 73.5$, $p = 0.04$), but no sex difference in fundamental frequency of whoops was evident among juveniles ($U = 87.5$, $p = 0.65$). The whoop bouts of juveniles had minimum fundamental frequencies nearly 50% higher than those of adults (juv: 379 ± 15; am: 265 ± 7, $U = 18$, $p < 0.0001$; af: 246 ± 6, $U = 7$, $p < 0.0001$). Therefore, listeners could potentially use minimum fundamental frequency to gain information about caller age until callers reached adulthood, and about caller sex thereafter.

Age/sex class had significant effects on whoop rate, mean whoop duration, mean inter-whoop interval and bout length, but not on the number of calls per bout (Table 3). We did not find significant differences between the acoustic parameters of bouts emitted by juvenile males and females (rate: $U = 75$, $p = 0.32$; duration: $U = 77.5$, $p = 0.36$; interval: $U = 75$, $p = 0.32$; length: $U = 63$, $p = 0.12$). This remained the case when context was controlled for by considering only whoops emitted during social excitement ($N_{jf} = 7$, $N_{jm} = 9$; rate: $U = 28$, $p = 0.76$; duration: $U = 25$,
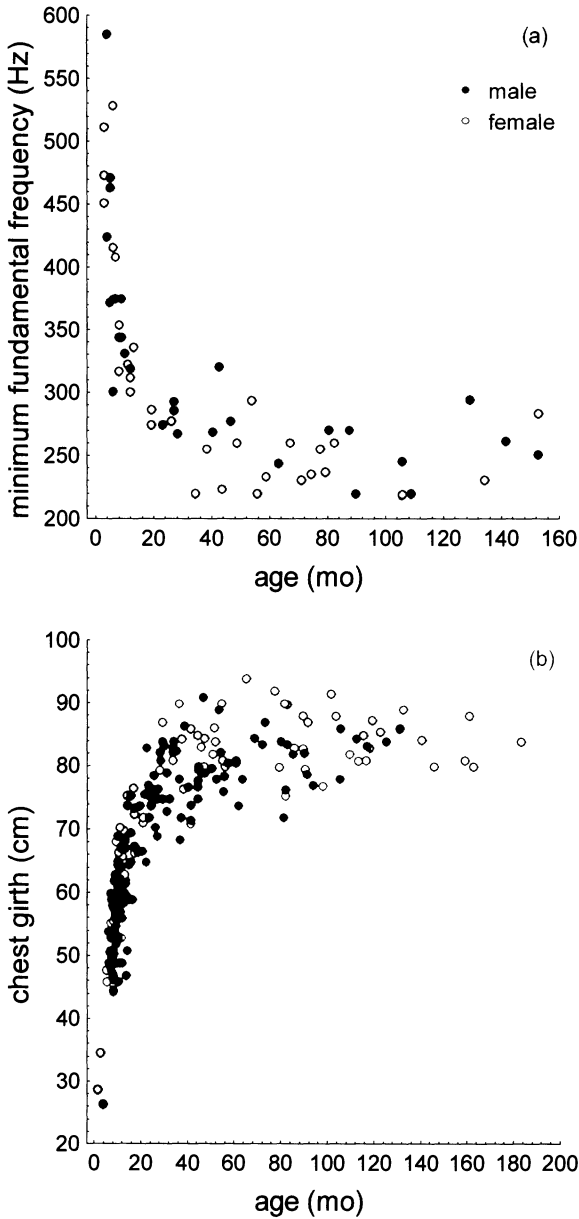
Figure 2. Variation based on age and sex in (a) minimum fundamental frequencies of whoop bouts and (b) chest girth.

Table 1. Fit of data documenting ontogenetic change in minimum fundamental frequency (F_0) and chest girth to the German Gompertz growth model for both male and female spotted hyenas. The AIC measures goodness-of-fit between the model and the data, while AC reflects whether serial autocorrelations exist among residuals of the model (Zelditch et al., 2003).

	N	AIC weight	AC	% Variance explained	Asymptote
Male					
Minimum F_0	28	0.315	NS	78.00	267.9 ± 11.3 Hz
Chest girth	148	0.145	NS	82.79	80.8 ± 0.8 cm
Female					
Minimum F_0	32	0.416	NS	86.99	243.4 ± 8.2 Hz
Chest girth	103	0.157	NS	88.87	84.1 ± 0.8 cm

Table 2. Summary of the piecewise linear regression analyses treating minimum fundamental frequency (F_0) and chest girth as a function of age, for both male and female spotted hyenas.

|	R	% Variance explained	Breakpoint	Approximate age at breakpoint (months)
Male				
Minimum F_0	0.905	81.91	320.7 Hz	12-16
Chest girth	0.917	84.15	68.0 cm	12-16
Female				
Minimum F_0	0.924	85.37	306.6 Hz	12-16
Chest girth	0.930	86.56	69.9 cm	12-16

$p = 0.54$; interval: $U = 31$, $p = 1.0$; length: $U = 30$, $p = 0.92$). There were also no apparent differences between the sexes in whoop parameters of juvenile bouts emitted spontaneously; however, the sample size for females was insufficient for us to draw statistical conclusions. After Bonferroni adjustments, we additionally found no significant sex differences in call structure between bouts by adults (rate: $U = 91$, $p = 0.26$; duration: $U = 109$, $p = 0.5$; interval: $U = 64$, $p = 0.03$; length: $U = 85$, $p = 0.11$). Controlling for context by considering only spontaneous whoops, inter-whoop intervals did not differ between adult males and females ($N_{am} = 13$, $N_{af} = 5$; $U = 22$, $p = 0.34$). Since there were no significant sex differences in the

Table 3. Summary of acoustic parameters for whoop bouts by juveniles, adult females and adult males. *p*-values are the products of Kruskal-Wallis ANOVA tests. Sample sizes represent the number of individuals sampled.

Bout parameter	Age/sex class	N	Mean $\pm$ SE	H-value	p-value
Whoop rate (calls/min)	juvenile female	15	25.45 ± 2.03	16.87	0.0008
	juvenile male	13	22.70 ± 1.13		
	adult female	16	18.72 ± 1.34		
	adult male	15	16.33 ± 1.17		
Inter-whoop interval (s)	juvenile female	15	1.85 ± 0.21	15.47	0.0015
	juvenile male	13	2.08 ± 0.16		
	adult female	16	2.38 ± 0.17		
	adult male	15	3.06 ± 0.24		
Call duration (s)	juvenile female	15	1.09 ± 0.09	12.19	0.0068
	juvenile male	13	1.16 ± 0.06		
	adult female	17	1.53 ± 0.12		
	adult male	15	1.44 ± 0.10		
Bout length (s)	juvenile female	15	19.32 ± 1.98	16.44	0.0009
	juvenile male	13	14.65 ± 1.36		
	adult female	17	21.67 ± 1.88		
	adult male	15	25.66 ± 1.86		
Calls per bout	juvenile female	15	7.85 ± 0.77	6.16	0.1040
	juvenile male	13	5.32 ± 0.50		
	adult female	17	6.44 ± 0.60		
	adult male	15	6.82 ± 0.62		

acoustic parameters of whoop bouts within each age class, we combined the sexes to evaluate effects of age on call structure.

Bouts emitted by juveniles were characterized by higher whoop rates, shorter call durations, shorter inter-whoop intervals, and shorter total lengths than those of adults (rate: $U = 175$, $p < 0.0001$; duration: $U = 219$, $p = 0.0005$; interval: $U = 211$, $p = 0.0005$; length: $U = 206$, $p = 0.0002$). Controlling for context by considering only spontaneous whoops, significant effects of age remained on inter-whoop interval and whoop rate ($N_{juv} = 11$, $N_{ad} = 19$: interval: $U = 44$, $p = 0.01$; rate: $U = 28$, $p = 0.0009$), although effects on call duration and bout length were not statistically significant (duration: $U = 63.5$, $p = 0.08$; length: $U = 60$, $p = 0.06$). Considering only bouts emitted during social excitement, the acoustic parameters of whoop bouts did not differ significantly between juveniles and adults after Bonferroni adjustments ($N_{juv} = 16$, $N_{ad} = 14$: rate: $U = 69$,
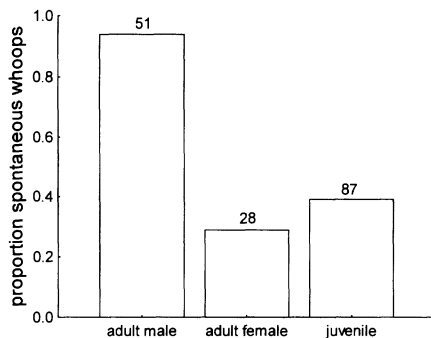
Figure 3. Comparison of the proportion of whoops emitted by adult male, adult female and juvenile spotted hyenas that occured in the absence of social excitement. The numbers above the bars indicate the number of whoop bouts sampled per age/sex class.

$p = 0.08$; duration: $U = 72$, $p = 0.1$; interval: $U = 81$, $p = 0.21$), although juvenile whoop bouts tended to be shorter than those of adults ($U = 54$, $p = 0.02$).

Effects of age and sex on whoop context

Juvenile males and females were equally likely to whoop in both contexts (chi-square test; $\chi^2_{1,87} = 1.25$, $p = 0.26$), so the sexes were combined for further analyses of whoop context. The probability of whooping in a given context varied among juveniles, adult males and adult females ($\chi^2_{2,166} = 22.05$, $p < 0.0001$; Figure 3). Juveniles ($\chi^2_{1,138} = 16.38$, $p < 0.0001$) and adult females ($\chi^2_{1,79} = 10.96$, $p < 0.001$) were much less likely to whoop spontaneously than were adult males. Juveniles and adult females, however, did not differ in the degree to which they whooped spontaneously ($\chi^2_{1,115} = 0.64$, $p = 0.42$).

Effect of call context on acoustic bout parameters

Whoop rates in sampled bouts did not demonstrate the bimodal distribution suggested by Kruuk's (1972) 'slow' versus 'fast' whoop dichotomy. Considering all recorded bouts, except for two containing a single call, whoop rates for both adult males and females exhibited normal distributions (Shapiro-Wilk's test; adult males: $N = 32$, $W = 0.95$, $p = 0.11$; adult females: $N = 21$, $W = 0.92$, $p = 0.07$). Among juveniles, whoop rates were not normally distributed, rather they were heavily skewed toward higher whoop
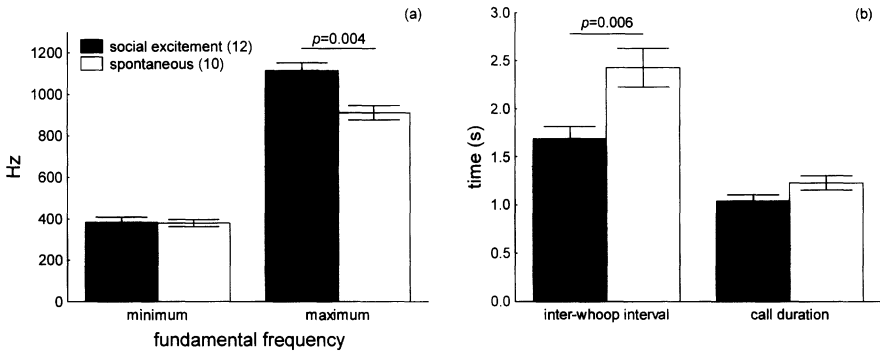
Figure 4. Variation in the (a) fundamental frequencies and (b) temporal parameters of whoop bouts emitted by juvenile spotted hyenas spontaneously and during social excitement. Sample sizes indicate the number of hyenas included in the analyses.

rates ($N = 62$, $W = 0.92$, $p < 0.001$). The rate at which calls were emitted in a whoop bout was affected by both the duration of individual calls within the bout ($F_{1,113} = 248.4$, $R^2 = 0.69$, $p < 0.001$), and the duration of inter-whoop intervals ($F_{1,113} = 803.9$, $R^2 = 0.88$, $p < 0.001$).

Although juveniles did not vary the minimum fundamental frequencies of their whoops with context ($N_{exc} = 12$, $N_{spon} = 10$, $U = 44$, $p = 0.31$), the peak fundamental frequencies of juvenile whoop bouts emitted during social excitement were approximately twenty percent higher than the frequencies of their spontaneous bouts ($U = 18$, $p = 0.004$; Figure 4a). Furthermore, juvenile whoop bouts emitted during social excitement had inter-whoop intervals approximately thirty percent shorter than did bouts produced spontaneously ($U = 19.5$, $p < 0.006$; Figure 4b). This resulted in a significant difference in whoop rate between the two contexts as well ($U = 22$, $p = 0.01$). Other parameters of juvenile whoop bouts were not observed to vary with context (duration: $U = 37.5$, $p = 0.14$; length: $U = 49$, $p = 0.5$; number: $U = 40.5$, $p = 0.2$). Context did not have a significant effect on the acoustic parameters of whoops emitted by adult females ($N_{exc} = 11$, $N_{spon} = 6$; minimum frequency: $U = 24.5$, $p = 0.4$; peak frequency: $U = 22$, $p = 0.3$; rate: $U = 17$, $p = 0.27$; duration: $U = 23$, $p = 0.35$; interval: $U = 14$, $p = 0.15$; length: $U = 31$, $p = 0.88$; number: $U = 17.5$, $p = 0.12$). Therefore, it appears that listeners could obtain information about the afferent state of juvenile callers from the maximum fundamental frequencies, inter-whoop intervals and whoop

rates of bouts, but that these acoustic parameters may not provide similar information about the affect of adult female callers.

Responses to whoops

An initial analysis of the 82 whoop bouts from archived field notes was conducted to determine whether or not listeners responded to whoops. We found no difference between the number of hyenas arriving on the scene before and after a whoop (Wilcoxon matched pairs: $Z = 0.32$, $p = 0.75$). However, significantly more approaches to the caller or its social partner occurred after whoops than before ($Z = 2.86$, $p = 0.004$). Therefore, for all subsequent analyses we considered a whoop to have received a response only if hyenas approached either the caller or a hyena who was interacting with the caller at the time the whoop occurred.

For 159 of the 166 bouts for which a spontaneous or social excitement context had been assigned, we were able to determine unambiguously whether or not the bout elicited a response from listeners. Juvenile males and females were equally likely to receive responses to their whoops (chi-square test; $\chi^2_{1,85} = 0.81$, $p = 0.37$). However, age and adult sex did affect the likelihood of clanmates responding to whoop bouts ($\chi^2_{2,159} = 8.79$, $p = 0.01$), with both juveniles ($\chi^2_{1,134} = 8.29$, $p = 0.004$) and adult females ($\chi^2_{1,74} = 6.25$, $p = 0.01$) receiving more responses to their whoops than adult males. Juveniles and adult females did not differ in the likelihood of hyenas responding to their bouts ($\chi^2_{1,110} = 0.007$, $p = 0.93$). However, whereas juvenile hyenas were nearly three times more likely to receive responses to whoop bouts emitted during social excitement than to those emitted spontaneously (logistic regression; Wald $\chi^2_{1,85} = 5.25$, $p = 0.02$; odds ratio $= 2.9$), adult females were equally likely to receive a response to whoops emitted in either context (Wald $\chi^2_{1,25} = 0.32$, $p = 0.57$).

For adult females, peak frequency, bout length, number of calls, whoop rate, call duration and inter-whoop interval did not affect the likelihood of conspecific response, as no parameter effects met the significance level criterion for entry into the multiple logistic regression model. For juveniles, inter-whoop interval was the sole bout parameter that significantly influenced conspecific response (Wald $\chi^2_{1,21} = 4.683$, $p = 0.03$; Figure 5). The model suggested that reduction of the inter-whoop interval by one second doubles the likelihood of listeners responding to juvenile whoop bouts (odds ratio
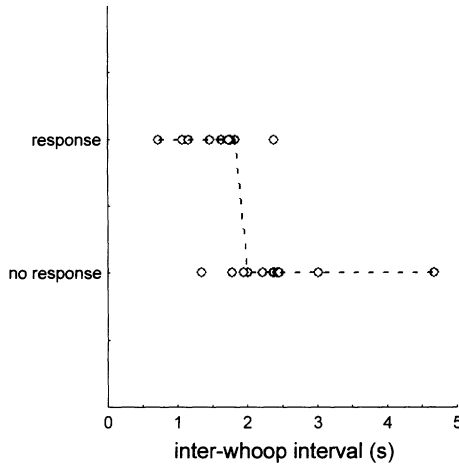
Figure 5. Average inter-whoop interval of whoop bouts emitted by juveniles, categorized by whether they did, or did not, elicit a response from conspecifics. A Lowess curve has been fit to the data (stiffness = 0.25).

= 0.036). This suggestion is potentially meaningful behaviorally, since in this analysis the range of inter-whoop intervals for juvenile bouts was 0.70-4.66 s, illustrating that a 1-s reduction in inter-whoop interval can certainly be achieved.

Use of asymmetric (A), symmetric (S) and terminal (T) whoop subtypes in bouts

All age/sex classes used A, S and T whoops in similar proportions within their bouts (Kruskal-Wallis ANOVA; A: $H_{3,60} = 0.17$, $p = 0.98$; S: $H = 0.27$, $p = 0.97$; T: $H = 1.84$, $p = 0.61$; Figure 6). Within bouts, type A whoops were used nearly twice as often as type S whoops (Wilcoxon matched pairs; $S = -413.5$, $p = 0.002$). Type T whoops occurred exclusively at the end of whoop bouts. Adult females did not vary their use of whoop subtypes with context (Mann-Whitney U test; $N_{spon} = 6$, $N_{exc} = 11$; A: $U = 22.5$, $p = 0.3$; S: $U = 23.0$, $p = 0.35$; T: $U = 32.0$, $p = 0.96$). Juveniles, however, did vary their use of type A and S whoops with context, using type A whoops twice as often, and type S whoops half as often, in whoops emitted during social excitement compared to those emitted spontaneously ($N_{spon} = 10$, $N_{exc} = 12$; A: $\overline{x}_{spon} = 0.4 \pm 0.12$, $\overline{x}_{exc} = 0.77 \pm 0.09$, $U = 26.5$, $p = 0.02$; S: $\overline{x}_{spon} = 0.54 \pm 0.12$, $\overline{x}_{exc} = 0.17 \pm 0.08$, $U = 29.5$,
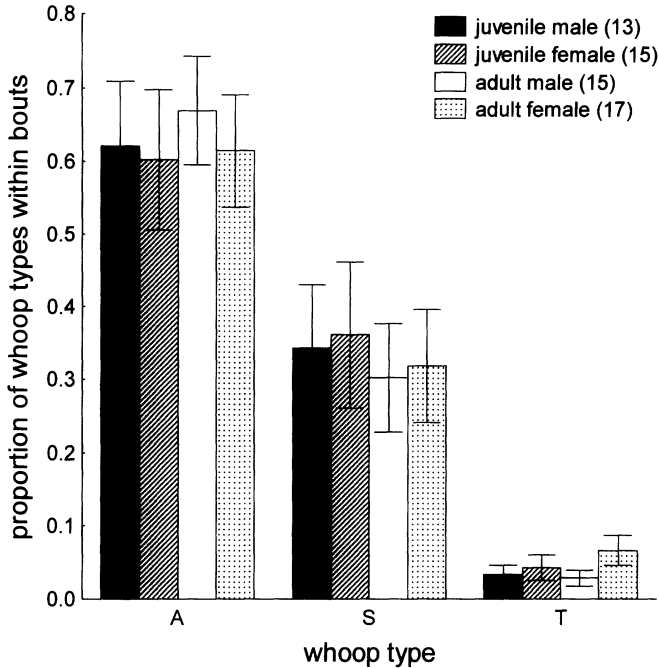
Figure 6. Proportion of asymmetric (A), symmetric (S) and terminal (T) whoops in whoop bouts emitted by each age/sex class. Sample sizes indicate the number of hyenas sampled per age/sex class.

$p = 0.04$). Juveniles did not vary their use of type T whoops with context ($U = 51$, $p = 0.58$).

To further evaluate whether hyenas use type A whoops to communicate urgency to clanmates, and thereby elicit support, we conducted additional logistic regression analyses in which we examined the effect of the proportional abundance of type A whoops in bouts on the likelihood of listener response. Including more type A whoops within bouts did not influence listener response to either adult female (Wald $\chi^2_{1,14} = 0.01$, $p = 0.91$), or juvenile whoop bouts (Wald $\chi^2_{1,21} = 0.03$, $p = 0.86$). A post hoc analysis of the effect of the proportion of type A whoops on inter-whoop interval revealed that varying the use of asymmetric whoops in bouts did not significantly affect inter-whoop interval (adult females: $F_{1,14} = 0.07$, $R^2 = 0.005$, $p = 0.8$; juveniles: $F_{1,26} = 0.19$, $R^2 = 0.007$, $p = 0.66$). Therefore, hyenas vary the inter-whoop intervals within bouts independent of whoop subtype.

Discussion

Effects of age and sex on call structure

Previous researchers have demonstrated that spotted hyena whoops convey information about age, sex and individual identity (East & Hofer, 1991a; Holekamp et al., 1999). East & Hofer (1991a) found that cub whoops typically contain fewer harmonics, wider spacing between harmonics, shorter durations of low frequency sections of calls, and higher minimum fundamental frequencies than do whoops of adults. Additionally, they reported that whoops emitted by adult males have higher fundamental frequencies than adult female whoops. We have replicated their finding that adult male whoop bouts have minimum fundamental frequencies intermediate between those of juveniles and adult females.

It has long been recognized that a vocalization's fundamental frequency can potentially serve as a gross, inverse cue to age and body size (Darwin, 1872; Morton, 1977; Hauser, 1993; Titze, 1994; Sousa-Lima et al., 2002; Reby & McComb, 2003; Pfefferle & Fischer, 2006). In most mammals, the fundamental frequencies of vocalizations are primarily determined by morphological characters such as glottal width, vocal chord length and length of the resonating tube (Michelsen, 1983). Although we were unable to obtain measures of these characters, our data suggest that, as chest girth (i.e., body size) increases during growth of spotted hyenas, the minimum fundamental frequencies of their whoop vocalizations correspondingly decrease. Playback experiments illustrated that spotted hyenas pay attention to age cues in whoops, as clanmates respond much more vigorously to whoops from younger callers than to those from older individuals (Holekamp et al., 1999). Although it remains to be determined whether hyenas utilize pitch cues to assess a caller's age, it would be surprising if they did not, as even humans can use the acoustic frequency of whoops to assign hyenas to broad age classes (Theis & Holekamp, unpublished data).

Effect of call context on call structure, and effects of call structure on response

We confirmed previous observations (Kruuk, 1972; East & Hofer, 1991b) that adult male spotted hyenas almost exclusively whoop spontaneously. Adult male whooping potentially advertises a male's presence in the territory to both prospective mates and male competitors (Mills, 1990). Adult

immigrant males queue for social status in a linear dominance hierarchy such that a male's position in the hierarchy is determined by the length of time he has spent in the clan, relative to the tenures of other adult male clan-mates (Smale et al., 1997; East & Hofer, 2001). For immigrant male spotted hyenas, length of residence in the clan has a large positive effect on reproductive success (Engh et al., 2002). By whooping, a male may simultaneously announce his presence to females and inform prospective immigrant males about male queue length within his clan (East & Hofer, 2001; Engh et al., 2002).

Adult female and juvenile hyenas also regularly whooped spontaneously, however, nearly two-thirds of their whoop bouts were emitted during periods of general excitement, in which the signaler usually exhibited postural cues indicating heightened arousal. Heightened arousal in other animals may be communicated vocally through increases in amplitude, fundamental frequency, call rate, and/or emission of a particular call subtype within a vocalization (Morton, 1977; Fichtel & Hammerschmidt, 2002). Without the aid of recording equipment, Kruuk (1972) reported that whoop bouts emitted during general excitement have increased vocal pitch and whoop rate; rate being a product of both reduced call durations and inter-whoop intervals.

In the current study, we did not find discrete, dichotomous 'slow' and 'fast' whoop subtypes (Kruuk, 1972), however, juvenile whoop bouts emitted during general excitement had higher maximum fundamental frequencies and shorter inter-whoop intervals than did spontaneous bouts. Although spotted hyenas generally utilize vocalizations other than whoops to signal danger, the attributes of whoops potentially indicating higher levels of arousal are similar to those frequently reported for the alarm calls of other species. For example, the alarm calls of redfronted lemurs, *Eulemur fulvus rufus*, emitted during intergroup encounters have higher frequencies than those given in response to less arousing stimuli (Fichtel & Hammerschmidt, 2002). Similarly, white-browed scrubwrens, *Sericornis frontalis*, employ higher-frequency alarm calls when predators are closer, and consequently the level of threat is greater (Leavesley & Magrath, 2005). Black-capped chickadees, *Poecile atricapilla*, reduce the inter-call intervals within their alarm bouts in the presence of smaller, more maneuverable and, consequently, more dangerous, raptors (Templeton et al., 2005). Meerkats, *Suricata suricatta*, encode information about urgency in their alarm calls by reducing both inter-call intervals and mean call durations within alarm bouts (Manser, 2001). Eastern

chipmunks, *Tamias striatus*, and yellow-bellied marmots, *Marmota flaviven-tris*, also increase their rate of alarm calling in high-threat situations (Burke da Silva et al., 1994; Blumstein & Armitage, 1997). Whereas alarm calls are typically only given in the presence of a predator and are usually simple in structure (Bradbury & Vehrencamp, 1998), mammalian loud calls, such as spotted hyena whoops, are more complex and may be emitted under a variety of circumstances. The long-distance 'wahoo' vocalizations of adult male baboons, *Papio cynocephalus*, are emitted at far greater rates during aggressive contests than comparatively low-arousal circumstances (Fischer et al., 2002). Among male baboons, an increased call rate is achieved con-comitantly with increased call duration, suggesting that the inter-call inter-val is greatly reduced in wahoos emitted during high-arousal situations, a phenomenon similar to that demonstrated by juvenile hyenas in the current study.

East & Hofer (1991b) categorized approximately one-half of spotted hyena cub whoops as either requests for support or attempts to attract the attention of the caller's mother. Here we found that one-half (43/85) of juve-nile whoop bouts did elicit a conspecific response, and that juvenile whoop bouts emitted during periods of heightened arousal were three times more likely to receive a response than those emitted spontaneously. Furthermore, we showed that, by reducing the inter-whoop intervals within bouts, juvenile hyenas greatly increased the likelihood of conspecifics responding to their whoops. It has been suggested that hyenas can reduce the inter-whoop in-tervals within bouts by using more asymmetric (A) whoops (East & Hofer, 1991a). Our data show, however, that hyenas vary the inter-whoop intervals within bouts independent of whoop subtype. Therefore, callers could po-tentially communicate urgency over long distances without sacrificing lo-calizability, as the characteristically longer symmetric (S) whoop subtype is more easily localized by listeners than the shorter type A whoop (East & Hofer, 1991b). This graded signal system may be particularly advantageous for animals living in fission-fusion societies, wherein allies may have to be recruited over considerable distances during inter- and intraspecific aggres-sion (Kruuk, 1972; Cheney & Seyfarth, 1990; Crockford & Boesch, 2003; Ramos-Fernandez, 2005; Slocombe & Zuberbuhler, 2005a).

Interestingly, we found that the acoustic parameters of whoop bouts emit-ted by adult female spotted hyenas did not differ between spontaneous and general excitement contexts. We believe it is highly unlikely that our results

are due to considering whoops that occurred under both aggressive and sub-
missive contexts together because whooping in aggressive contexts is very
rare (East & Hofer, 1991b). Of the 20 adult female whoop bouts emitted
during general excitement in the current study, only one was by a hyena
who had just directed aggression at a conspecific. It is possible that adult fe-
male hyenas communicate information about their affective state, as do other
species, through non-temporal acoustic parameters such as harmonics, with
harsh, noisy vocalizations indicating a high level of arousal (Morton, 1977;
Manser, 2001; Soltis et al., 2005). It may also be that, in defining context as
either spontaneous or general excitement, we have not accounted fully for
the social complexity experienced by adult female spotted hyenas.

It has been suggested that the primary function of whooping for adult
spotted hyenas is self-advertisement (Mills, 1990; East & Hofer, 1991b). Our
findings confirm that for adult males this is most likely the case, as nearly all
their whoops were spontaneous. However, less than thirty percent of adult
female whoop bouts were emitted spontaneously. Additionally, we have po-
tentially underestimated whooping under conditions of general excitement
in this study by necessarily excluding all whoop bouts that were preceded or
followed within 10 min by other whoop vocalizations. Concurrent whooping
by multiple adults occurs during lion-hyena interactions, as well as during
border disputes with neighboring hyena clans (Kruuk, 1972; Mills, 1990;
East & Hofer, 1991b). Within our *Crocuta* study population, the frequency
of whooping by adult females is three times greater in the presence of lions
than in their absence (Theis, unpublished data). In the current study, one-fifth
(4/20) of the adult female whoop bouts emitted during general excitement
occurred during conflicts with lions. If it were possible to control for the po-
tentially additive effects of concurrent whooping, examining a larger dataset
might reveal that adult females do vary the parameters of their whoop bouts
between contexts, and that this variation does influence conspecific response,
including the arrival onto the scene of hyenas who were not present at the
time of the whoop. Previous researchers have described situations in which
whooping by adult females appeared to function in recruiting clanmates dur-
ing lion-hyena conflicts (Mills, 1990; East & Hofer, 1991b). Similarly, we
have seen as many as 56 hyenas recruited rapidly to interactions with multi-
ple lions when several female hyenas whooped in quick succession (unpub-
lished data).

East & Hofer (1991b) noted that whooping by adult females may func-
tion not only to recruit conspecifics during lion-hyena conflicts and border
disputes, but also to discourage further aggressive attacks on the caller by
clanmates. In this study, approximately one-half (11/20) of the adult female
whoop bouts emitted during general excitement occurred just after the caller
had been aggressed upon by one or more clanmates. This suggests that adult
female hyenas probably often whoop to request support or to remind aggres-
sors of the caller's identity (East & Hofer, 1991b). It also suggests that our
sample size for recorded adult female whoop bouts may have been insuffi-
cient to pick up differences in acoustic parameters between spontaneous and
general excitement contexts.

Although adult females in this study did not vary the acoustic parameters
of their bouts by context, juveniles did. While increasing the pitch and pro-
portional abundance of asymmetric whoops in bouts did not effectively elicit
conspecific response, clanmates were much more likely to respond to juve-
niles who reduced the inter-whoop intervals of their bouts. This suggests that
the inter-whoop intervals of juvenile whoop bouts reflect the degree of caller
arousal in functionally meaningful ways. In the future, our findings should
be supplemented with playback experiments to free-living spotted hyenas in
which the length of the inter-whoop interval is manipulated. If hyenas re-
spond more frequently, or more strongly, to bouts with reduced inter-whoop
intervals, it will conclusively demonstrate that temporal variation in whoop
bouts communicates meaningful information to receivers about caller affect.

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