Long-distance communication facilitates cooperation among wild spotted hyaenas, *Crocuta crocuta*

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Calls that catalyse group defence, as in the mobbing of predators, appear to facilitate cooperation by recruiting receivers to act collectively. However, even when such signals reliably precede cooperative behaviour, the extent to which the calls function as recruitment signals is unclear. Calls might simply arouse listeners' attention, setting off a cascade of independent responses to the threat. By contrast, they might convey information, for example, about signaller identity and the nature of a threat that affects receivers' decisions to participate. We explored this distinction by investigating a possible long-distance recruitment call used by spotted hyaenas. These social carnivores live in fission–fusion clans and individuals disperse widely within their territories. Putative recruitment calls must therefore attract receivers that are distant from the inciting threat and free to opt out of risky collective aggression. Hyaenas compete with lions over food, and neighbouring clans sometimes engage in violent border clashes. These high-stakes contests are decided based on numerical asymmetries, so hyaenas can only protect critical resources if the dispersed clan can converge quickly at conflict sites. We recorded and analysed whoop bouts produced in multiple contexts and found that bouts produced in response to signs of lion–hyaena conflict had shorter inter-whoop intervals than spontaneous 'display' bouts. In subsequent field playback experiments, resting hyaenas were significantly more likely to move in response to 'recruitment' bouts with shortened intervals than to otherwise identical 'display' bouts. Whereas only stimulus type predicted movement, lower-ranked subjects responded most quickly, perhaps because their feeding opportunities depend on arriving early at any kill site. Results demonstrate that hyaenas possess a signal that can reliably recruit allies across long distances, despite moderating effects of individual circumstances on the strength of receivers' responses.

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Individuals of many species vocalize when they perceive a threat. 'Alarm calls', the broadest term for this type of vocalization, are among the best-studied animal signals, in part because they offer insight into the evolution of cooperative behaviour (Searcy & Nowicki, 2005). Alarm calls may originate as affective vocal responses to danger, but natural selection appears to have shaped basic distress calls into diverse and sophisticated behaviours that benefit callers and receivers alike. Callers may increase their own risk of detection when they vocalize, but pervasive audience effects

suggest calling is under voluntary control, as individuals are more likely to produce alarms when they can enhance their own fitness by warning relatives or close associates of a threat (Cheney & Seyfarth, 1985; Karakashian, Gyger, & Marler, 1988; Le Roux, Cherry, & Manser, 2008; Seyfarth & Cheney, 2012; Sherman, 1977). Receivers may modify their responses depending on the identity of the caller or the particular threats associated with particular forms of alarm (Zuberbühler, 2009). Some specialized alarms appear to incite receivers to join a collective assault on the threat, rather than to flee. These vocalizations are often termed 'recruitment calls' when they draw conspecifics to a particular location, and 'mobbing calls' when they precede or directly accompany other forms of defence behaviour. Mobbing and recruitment calls are widespread among birds (Curio, 1978;

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Dugatkin & Godin, 1992; Krams, Krama, Igaune, & Mänd, 2007), primates (Clara, Tommasi, & Rogers, 2007; Meno, Coss, & Perry, 2013) and social carnivores (Furrer & Manser, 2009; Graw & Manser, 2007). Studies in these systems have explored a range of evolutionary explanations for the behaviour of both callers and receivers, from reciprocal altruism (Krams et al., 2007) to by-product mutualism (Russell & Wright, 2009). However, the role that vocalizations play in catalysing group defence is difficult to disentangle from influences of other stimuli, including the immediate presence of the threat itself (Ostreiher, 2003). Ambiguity about the functional role of vocalizations in group defence contributes to further ambiguity about the mechanisms by which calls might facilitate collective action (e.g. by transmitting arousal, providing information, or both, Seyfarth et al. 2010). The distinct nature of mobbing and recruitment calls therefore remains in question. Are these vocalizations distinct tools that catalyse cooperative defence, perhaps shaped by natural selection to perform that function? Or are such calls general alarms that merely co-occur with collective behaviour?

To examine the specific function of vocalizations within cooperative defence, we investigated a putative recruitment call in a fission—fusion society, wherein group members are widely dispersed. While visual displays and the physical presence of the inciting threat itself often co-occur with vocalizations when callers and receivers live in stable social groups, such cues will often be unavailable to receivers in species that live in fission—fusion societies. If long distances separate dispersed group members, calls will often reach distant receivers unaccompanied by other auditory, visual or olfactory information from either the caller or the threat. In these contexts, vocal signals alone must suffice to initiate collective defence behaviour and to attract and sustain receivers' attention and motivation until they reach the caller. Recruitment, in other words, would appear to be a distinct and necessary phase of collective defence under such conditions, and might require a correspondingly distinct 'recruitment call'. For a long-distance recruitment call to be evolutionarily stable, it would need to not only announce the caller's distress but also elicit cooperative responses from group-mates who hear the call at varying distances, in varying circumstances, and who have the choice to opt out of risky collective action.

We investigated the possible use of a long-distance recruitment call among spotted hyaenas, *Crocuta crocuta*, gregarious social carnivores whose societies and ecology would seem to demand that they coordinate collective action across large distances. Hyaena clans can contain up to 90 individuals (Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012), but rank-mediated aggression and rank-based priority of food access (Frank, 1986; Smith, Kolowski, Graham, Dawes, & Holekamp, 2008; Tilson & Hamilton, 1984) cause individual members to spend much of their time foraging alone or in small subgroups (Holekamp, Smale, Berg, & Cooper, 1997; Smith et al., 2008). Over 87% of hunts are conducted by just one or two hyaenas (Holekamp et al., 1997), and lower-ranked hyaenas hunt in significantly smaller subgroups than do their higher-ranked clanmates (Holekamp et al., 1997; Smith et al., 2008). Females also seek isolation to give birth, allowing cubs to spend the first weeks of life away from aggressive interactions at the communal den (Drea, Hawk, & Glickman, 1996; East, Hofer, & Turk, 1989). The tendency of individuals to disperse, combined with geographically large territories (clans of 15 or fewer individuals can occupy territories of >1500 km^2, Mills, 1990) can mean that even large clans will be highly diffuse. However, hyaenas must also regularly gather to cooperatively defend food or territorial boundaries against lions, *Panthera leo*, or rival clans (Hofer & East, 1993; Kruuk, 1972; Smith et al., 2008). Numerical asymmetries can determine the outcomes of these clashes, most evidently in the case of food competition with lions: hyaenas can only defend or steal kills from lions at ratios of at least four adults for every adult female or subadult lion present (Benson-Amram, Heinen, Dryer, & Holekamp, 2011; Cooper, 1991; Trinkel & Kastberger, 2005).

Given the intense pressures on hyaenas both to disperse widely and converge rapidly, a call to 'rally the troops' would clearly be advantageous in this species. Past observations suggest that the long-distance 'whoop' vocalization performs this function. During conflict with lions and neighbouring clans, hyaenas produce series of whoops (called bouts) that seem to attract other clan members (East & Hofer, 1991a; Kruuk, 1972; Mills, 1990). Whoop bouts have an estimated range of 5 km and contain a mixture of high-frequency elements and stacked harmonics that may make them localizable over long distances (East & Hofer, 1991b), and experimental evidence suggests that hyaenas are able to discriminate between whoops of individual callers (Benson-Amram et al., 2011; Holekamp et al., 1999). However, the role of whoop bouts in group defence has not been clear. This is partly because hyaenas produce whoop bouts in a wide variety of contexts, and the strength of observed responses to such bouts varies widely (Mills, 1990; Ogutu & Dublin, 1998). Most bouts are not preceded by any observable stimulus and elicit little or no response from clanmates. Observers have therefore proposed that these spontaneous bouts must function as displays, perhaps allowing dominant females to advertise their physical formidability, males to advertise themselves to reproductive females, or members of neighbouring clans to assert territorial ownership (East & Hofer, 1991a; Mills, 1990). Observations of hyaenas' responses to whoops from an unseen caller further suggest that the majority of whoop bouts are low-urgency displays: hyaenas treat most of these bouts with apparent indifference (67.6% in Mills, 1990). In contrast, a minority of whoop bouts elicit immediate movement, usually towards the source but occasionally directly away from it (17.5% and 0.8%, respectively, in Mills, 1990). The variation in receivers' responses, and the wide range of contexts in which hyaenas produce whoops, have led observers to posit multiple distinct functions for whooping. Bouts produced in contexts such as mother—cub exchanges, cross-border interclan display contests and direct conflicts over kills (East & Hofer, 1991a, 1991b; Kruuk, 1972; Mills, 1990; Theis, Greene, Benson-Amram, & Holekamp, 2007) may all be functionally distinct, but the possibility that whoops with specific acoustic qualities might function as recruitment calls has never been assessed experimentally.

Hyaenas' ecology also appears to complicate the task of recruiting groupmates for collective defence, as the balance between the costs and benefits of responding to a recruitment call vary widely among individual receivers. Large, contested carcasses offer potential feeding opportunities to lower-ranked clan members that might be excluded from smaller kills (Smith et al., 2008), and territorial defence ultimately maintains every clan member's access to critical resources (Boydston, Morelli, & Holekamp, 2001; Van Horn, Engh, Scribner, Funk, & Holekamp, 2004). However, severe injuries and fatalities can occur at conflicts over food (East & Hofer, 1991a; Kruuk, 1972), and lions represent a leading cause of hyaena mortality (Watts & Holekamp, 2008). Kinship or close association with the caller might induce some individuals to respond to a recruitment call (but see Schibler & Manser, 2007). However, genetic relatedness across matrilines within clans is highly variable (Van Horn et al., 2004) and it is probable that many potential receivers of a given recruitment call are only distantly related to the caller (Engh et al., 2002; Szykman, Van Horn, Engh, Boydston, & Holekamp, 2007; Van Horn et al., 2004). Therefore, the energetic costs and physical risks associated with investigating a distant whoop or joining a potentially lethal contest must be balanced against benefits that vary with individual rank, relatedness and distance from the caller (Smith et al., 2008). Indeed, although three

times as many clan members participate in cooperative defence as in other collective behaviours such as hunting (Van Horn et al., 2004), individual hyaenas vary in the intensity of their participation. Boydston et al. (2001), for example, found that females were more likely than males to participate in risky front-line attacks against rival clans.

The hyaenid system offers an opportunity to investigate a possible recruitment call that is (1) received in the absence of visual or other cues from an inciting threat and (2) processed by receivers that are free to demonstrate a range of responses. To test the hypothesis that hyaenas produce a distinct variant of the whoop bout that recruits receivers to the caller's location, we first recorded whoop bouts in likely 'display' and 'recruitment' contexts and analysed the two sets of recordings for context-specific variation. Upon finding that bouts from recruitment contexts had significantly shorter inter-whoop intervals than putative display bouts, we manipulated the durations of intervals in recorded bouts from known callers to create matched pairs of playback stimuli ('Recruitment type' and 'Display type'), and conducted field playback experiments testing whether bouts with shorter intervals were more likely to elicit movement from subjects. Given both the external pressures on clanmates to cooperate against competitors and the autonomy granted individual group members by fission–fusion dynamics, we predicted that Recruitment stimuli would induce subjects to leave their resting locations, but that social rank, which affects the costs and benefits attached to participating in collective aggression, would influence the strengths of subjects' responses.

PART 1: EXPLORATORY RECORDING AND ACOUSTIC ANALYSIS OF WHOOP BOUTS

In 2010 we recorded two sets of whoop bouts in two distinct contexts. The first consisted of spontaneous 'display' bouts, collected ad libitum during morning and evening observation sessions. We categorized these as 'displays' because they were not produced in response to any observable alarming stimuli and did not elicit strong reactions from any other observable hyaenas, in conformity with prior observers' descriptions of whoop bouts that appeared to serve a display function (East & Hofer, 1991a; Henschel & Skinner, 1991; Kruuk, 1972; Mills, 1990; Theis et al., 2007). The second set of bouts consisted of putative recruitment calls elicited from hyaenas in simulated conflicts between hyaenas and lions (see Methods, Recording whoop bouts), a context within which prior observers reported whooping that appeared to recruit receivers to the caller's location (East & Hofer, 1991a; Henschel & Skinner, 1991; Kruuk, 1972; Mills, 1990; Theis et al., 2007).

We next analysed field recordings of the putative display and recruitment whoop bouts for structural variation corresponding to recording context. We focused on two acoustic parameters that prior studies have associated with bouts produced in contexts involving within- and cross-species aggression: the duration of inter-whoop intervals and the predominance of 'type A' (asymmetrical) whoops (whoops that rise to a final peak frequency, as in Fig. 1a). Multiple observational surveys (Kruuk, 1972; Mills, 1990) describe a 'fast' whoop-bout variant with a higher whooping rate produced in response to aggression. East and Hofer (1991b) further proposed that bouts produced in agonistic contexts might feature more type A (whoops 1–3 in Fig. 1a) whoops, whose asymmetric structure, as compared to lengthier, symmetrical 'type S' whoops (whoops that rise and fall around a central peak frequency), might lend itself to rapid production. A later analysis by Theis et al. (2007) found mixed support for the relationships between structural features and calling contexts proposed by prior observers. In Theis's sample, juveniles' bouts produced in response to 'social excitement'

had shorter intervals and more type A whoops, and these bouts were more likely to attract attention from adult receivers. However, these findings did not hold for whoops produced by adults. Theis also found that interval durations and distributions of whoop types varied independently of one another. Given the lack of full consensus in the literature, we focused our structural analysis on acoustical parameters that might increase within-bout call rate, treating both inter-whoop interval and whoop type as viable candidates for context-based variation.

Methods

Subjects and study site

Field recordings were collected from February to July 2010 in the Mara Triangle, the northwestern region of the Maasai Mara National Reserve in southwest Kenya, administered by the Mara Conservancy. We recorded vocalizations and accompanying behavioural observations of hyaenas in five clans in the Mara Triangle that have been studied by the Michigan State University Mara Hyena Project since 2008 (the North, South, Happy Zebra, 17 Kilometre (17 KM) and Oz Valley clans). These clans ranged in size from 16 to 58 known members (average group size = 39 members) at the time of this study. Sex of individual hyaenas was determined by the dimorphic shape of the glans of the erect phallus (Frank, Glickman, & Powch, 1990); age of all known individuals could be estimated to within ± 7 days (Holekamp, Smale, & Szykman, 1996). We considered hyaenas to be juveniles up to 24 months of age and adults thereafter. We identified individuals by their unique spot patterns and other natural features.

Recording whoop bouts

All recordings were made from research vehicles with engines off, using Sennheiser ME66 shotgun microphones with foam windscreens and Marantz PMD 661 portable solid-state digital recorders at a sample rate of 48 kHz and a resolution of 24 bits.

Ad libitum recording during field observations. We recorded all whoop bouts that occurred during 187 morning (0500–1000 hours) and evening (1630–2000 hours) field-observation sessions (sessions were distributed evenly across morning and evening blocks), including bouts produced by focal hyaenas visible from the observation vehicle and any audible bouts from 'distant' callers (callers out of view of observers, including nearby callers fully obscured by intervening features of the landscape). For each recorded call we collected data on the reactions of all hyaenas visible to observers, including approaches or other responses to the caller when the vocalizing animal was in view, and looks, movement, answering vocalizations or other reactions when the source of the call was distant.

Recording of whoops at simulated lion–hyaena conflicts. To collect whoop bouts produced in the context of conflict, we exposed hyaenas to a simulated conflict event using a 'call-in' procedure. Call-ins involve broadcasting recorded vocalizations from a conflict in order to attract resident carnivores to the broadcast site (Mills & Hofer, 1998; Ogutu, Bhola, & Reid, 2005; Ogutu & Dublin, 1998). We used recordings of a large group of lions and hyaenas fighting over a kill, originally collected in the Moremi Game Reserve in Botswana, as call-in stimuli. Prior work using similar methods has consistently shown that hyaenas respond as strongly to the sounds of such call-ins as they would to real clashes between lions and hyaenas, and that they approach the broadcast site from distances of up to several kilometres away, arriving highly aroused and in some cases whooping themselves (Boydston, 2001; Mills & Hofer, 1998; Ogutu et al., 2005; Ogutu & Dublin, 1998).
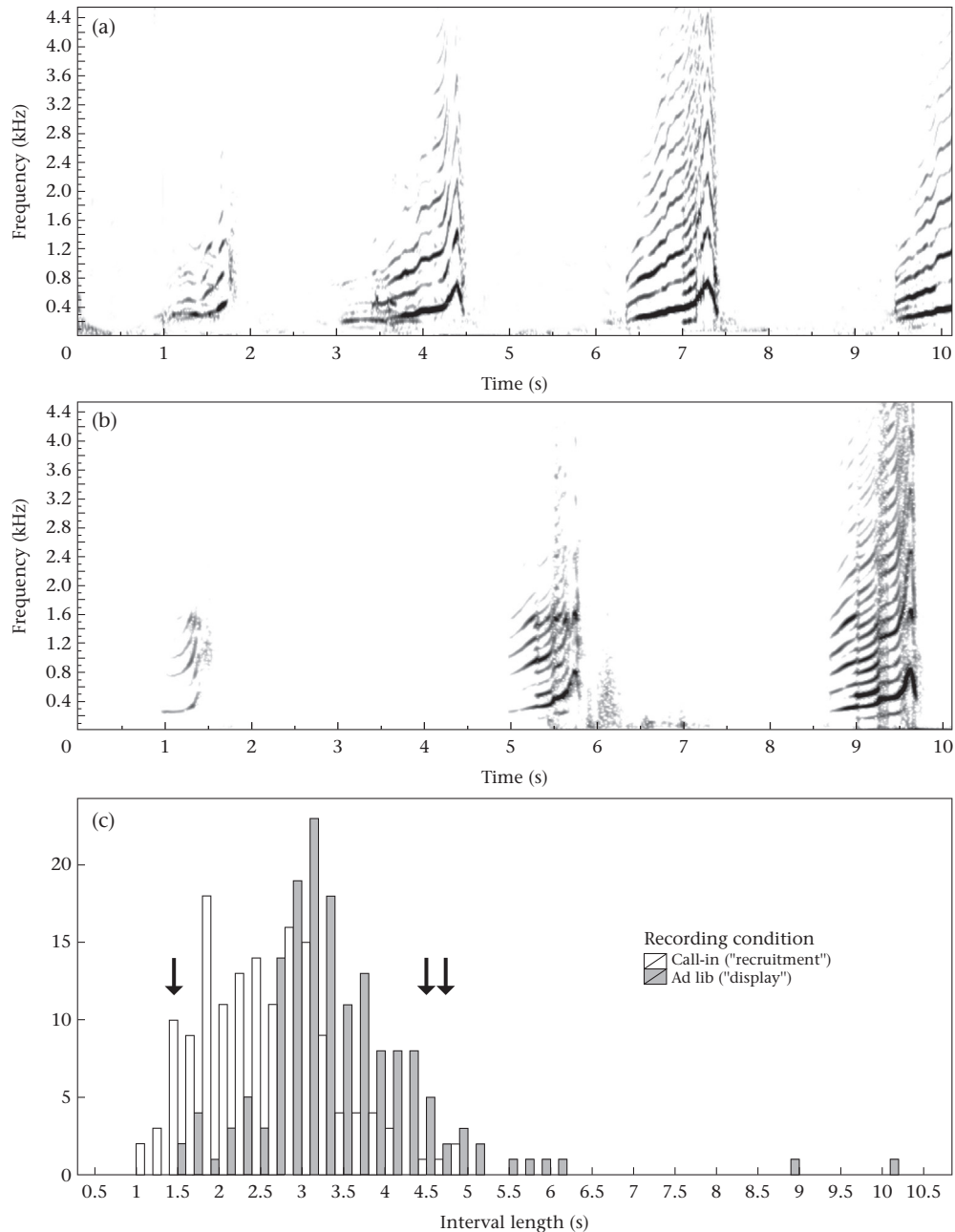
Figure 1. Spectrograms showing the first 10 s of (a) 'recruitment' and (b) 'display' whoop bouts recorded in the field, illustrating the difference in typical inter-whoop interval durations for these types of bouts. The recruitment bout in (a) was elicited at a call-in (i.e. simulated lion–hyaena conflict) from the adult female SNAP (mean interval duration: 1.9 s). The display bout in (b) was produced spontaneously by the adult male RSTR at an observation session and recorded ad libitum (mean interval duration: 2.9 s). From within the observed distributions of interval durations for all 'recruitment' and 'display' recordings (c), we selected durations of 1.5 s and 4.5 s (the single ↓ and double ↓↓ arrows, respectively) as baseline interval lengths when constructing Recruitment and Display playback stimulus bouts.

We conducted 40 call-in trials, distributed mainly amongst the three study clans whose territories were most accessible (15, 11 and 9 trials in the Happy Zebra, North and South clan territories, respectively) with five additional trials in the more distant territories of the 17KM and Oz Valley clans. We followed a standard protocol for all trials. After arriving at a location within a clan's territory and noting that no hyaenas were visible in the vicinity, we broadcast one of two recordings of lions and hyaenas fighting (or both in succession). Playbacks were broadcast using an Apple iPod (5th generation, 60 GB, model A1136) and Altec-Lansing iMT800 Portable Digital Boom Box, with volume set to maximum on both the iPod and the iMT800. Speakers were placed

on the roof of the car. We played the recording one to five times (average recording length: 5.5 min; median of three plays per call-in), rotating speakers to face a different direction with each play. We stayed at call-in sites for a minimum of 15 min and an average of 30 min after the onset of the first playback. We did not conduct call-ins during rain. To reduce habituation to our stimuli, we rotated call-in trials across all five clans' territories and, within each territory, chose staging sites for each successive trial that were as distant as possible from prior sites. When listeners' responses began to show signs of habituation (e.g. when the majority of respondents arrived at the call-in site at a walking pace rather than the typical lope), we ceased trials in that clan's

territory. No whoops were recorded after hyaenas showed signs of habituation.

Analysis of inter-whoop intervals and whoop types

Whoop-bout recordings were analysed using Praat v. 5.1.30 (Boersma & Weenink, 2010) to visualize all bouts and to measure durations of whoops, intervals and bouts. We examined each whoop in every bout by eye and categorized it as type A, S or T (the rare 'terminal' whoop that appears only at the end of some bouts).

Results

Ad libitum recordings (display context)

Ad libitum recording sessions yielded a total of 22 whoop bouts (from 22 independent incidents) of sufficient quality for acoustic analysis. The bouts were recorded from individuals of the South (13 bouts), North (6 bouts) and 17 KM (3 bouts) clans. In five cases (2 adult females, 2 adult males and 1 subadult of unverified sex) we observed the caller and were able to confirm that the context of vocalization was consistent with prior descriptions of spontaneous display whooping (East & Hofer, 1991a; Kruuk, 1972), because no obvious stimulus provoked the caller to whoop. The remaining 17 bouts were from callers that were out of sight at the time of vocalizing. Although we could not verify the caller's immediate context in these 17 cases, none of these bouts provoked strong responses from other hyaenas, leading us to classify them as display bouts. If this classification was incorrect and there were any recruitment bouts among these calls, we reasoned that this could only bias our analysis against finding a distinction between these bouts and the ones recorded at call-ins.

Call-in recordings (lion–hyaena conflict context)

At least one respondent whooped during 15 of the 25 (60%) call-ins that attracted hyaenas. Bouts came from 18 known unique individuals and seven individuals whose identity could not be verified at the time of recording. We recorded a total of 25 whoop bouts during call-ins that were of sufficient quality to analyse acoustically. The 25 recorded bouts came from callers that were predominantly adult (17 verified adults, 1 juvenile, 7 unidentified) and female (12 female, 5 male, 1 known individual of unknown sex, 7 unidentified). Whoops were recorded from individuals of the South (11 bouts), North (7 bouts), 17 KM (4 bouts) and Happy Zebra (3 bouts) clans.

Concurrent behavioural observations supported our expectation that hyaenas, including those that vocalized, responded to the call-ins as they would to actual lion–hyaena conflicts. At least one hyaena came to the broadcast site in 25 of the 40 trials (63%), and the mean number of respondents for successful call-ins was five. As in previous studies (Ogutu & Dublin, 1998; Ogutu et al., 2005; Webster, McNutt, & McComb, 2010), hyaenas responded strongly to the call-ins and consistently arrived at broadcast sites behaving as though they regarded the stimuli as evidence of a highly salient event. Call-ins drew hyaenas from more than a kilometre away (as observed in multiple trials where distant resting hyaenas were observable from the broadcast site). In 25 call-ins that attracted at least one hyaena, 91% of respondents whose arrival was observed ($N = 110$) arrived at a lope; another 17 respondents were first noted after they had already arrived. In addition to searching persistently around or past the broadcast vehicle, respondents showed signs of excitement such as arriving with tails erect and bristled, producing alarm rumbles and depositing paste (Kruuk, 1972; Mills, 1990; Woodmansee, Zabel, Glickman, Frank, & Keppel, 1991). We recorded any whoop bouts produced during the period from the first approach of individuals arriving at the call-in site until the cessation of these searching behaviours.

Acoustic analysis

Bouts elicited at call-ins ($N = 25$) and those recorded ad libitum ($N = 22$ bouts) showed no significant difference in the proportion of type A and type S whoops within bouts (mean $\pm$ SE proportion of type A whoops per bout: call-in bouts: 0.73 ± 0.28; ad libitum bouts: 0.74 ± 0.30; unpaired t test: $t_{46} = -0.13$, $P = 0.89$). However, the inter-whoop intervals in the putative recruitment whoop bouts produced at call-ins were shorter than those produced in display whoop bouts (mean $\pm$ SE interval length: call-in bouts: 2.55 ± 0.78 s; ad libitum bouts: 3.44 ± 1.07 s;). Because multiple intervals were obtained from the same recording event (bout), such that some events and some individuals contributed disproportionately to the pooled data, we used a log-transformed linear mixed model to test for significance. Fixed effects of recording context (recruitment/ call-in versus display/ad libitum) and interval number (each interval's place, e.g. first, second, etc., within a bout) were included, as well as random intercepts for individual callers and for individual bouts. Results showed that recording context was associated with a $1.3\times$ difference in interval duration. A likelihood ratio test comparing nested models with and without the recording context predictor revealed that the model including recording context was the better model ($\chi^2_6 = 4.56$, $P < 0.033$).

The pattern in our recordings matched the pattern reported by previous observers of whooping behaviour, as well as the pattern Theis et al. (2007) found for juvenile vocalizations: shorter inter-whoop intervals in the recruitment (call-in) bouts resulting in a faster whooping rate. We therefore proceeded, in the second phase of research, to experimentally test the functional value of inter-whoop interval duration. We did this by constructing a set of playback stimuli in which we manipulated just one parameter in a subset of our recorded bouts: the duration of inter-whoop intervals.

PART 2: PLAYBACK EXPERIMENTS

Methods

Subjects

Playback experiments were conducted from September 2010 to January 2011 and September to December 2011 in the Mara Triangle. We conducted playbacks only on lone adult hyaenas at rest far from active den sites or other visible clanmates. Because such subjects could be difficult to locate, we restricted our search to two hyaena clans whose territories were most accessible to researchers. Playback subjects were 30 adult (>24 months) members of the North ($N = 8$ subjects) and South ($N = 22$ subjects) hyaena clans, which have been continuously monitored by the Michigan State University Hyena Project since 2008. Identities of all clan members and composition of matrilines were known. At the time of the experiments, the North clan had 27 adult natal clan members and nine resident immigrant males; the South clan had 29 adult natal clan members and nine resident immigrant males. We determined the social ranks of all adults in each clan using a matrix of outcomes of dyadic, agonistic interactions, including unsolicited appeasement behaviour (Smale, Frank, & Holekamp, 1993), collected by all-occurrence sampling (Altmann, 1974). To determine the abundance of prey, which was one of the factors we considered a possible predictor of subjects' responses to playback stimuli, populations of ungulates and other prey species were censused biweekly by counting animals within 100 m of three 4 km transect lines. Prey abundance fluctuated significantly with the presence or absence of large herds of zebra and wildebeest that migrate periodically through the Maasai Mara (Broten & Said, 1995; Cooper, Holekamp, & Smale, 1999) on their way to and from the Serengeti (mean $\pm$ SE number of

prey animals counted during the migration period: 381 ± 81; mean $\pm$ SE during the rest of the year: 54 ± 6; Welch test: $t_{40.4} = 4.0$, $P < 0.001$).

Construction of playback stimuli

Based on the results of our acoustic analyses, we constructed matched pairs of long-interval (hereafter referred to as Display) and short-interval (hereafter referred to as Recruitment) playback stimulus bouts that were constructed from the same call (thus controlling for caller identity) and differing only in the durations of inter-whoop intervals. To control for any context-based variation in acoustic parameters other than interval length, we used only the bouts recorded at call-ins to construct playback stimuli. We began with nine bouts from nine unique individuals (eight adult females and one adult male). We edited each bout to create a matched pair of stimuli: one Display stimulus with lengthened intervals and one Recruitment stimulus with shortened intervals. Following Fischer, Metz, Cheney, and Seyfarth (2001), we selected inter-whoop interval lengths for the Display and Recruitment stimuli that (1) fell within the range of naturally occurring calls from our original recordings and (2) skewed towards the categorically distinct ends of the spectrum of interval durations: an initial interval of 1.5 s for Recruitment stimuli and 4.5 s for Display stimuli (Fig. 1c). A log-transformed linear model of interval lengths for all recordings showed that intervals elongate steadily within a call bout, with each successive interval 1.017x the duration of its predecessor. We used this pattern to vary interval length naturalistically within the stimuli. This process produced a total of nine matched stimulus pairs (Fig. 1a, b).

We used Adobe Audition software (v. 1.5, Adobe Systems Inc., San Jose, CA, U.S.A.) to create stimuli. For all Recruitment stimuli, the first interval was set at 1.5 s and each subsequent interval was 1.017x the length of the previous one (1.5 s, 1.525 s, 1.551 s, etc.). For Display stimuli, the first interval was set at 4.5 s and each subsequent interval was 4.576 s, 4.653 s, etc. Whenever an interval in the original recording had to be lengthened in order to fit the standardized template of interval lengths, we did so by inserting a section of low-volume environmental sound cut and pasted from elsewhere in the same recording.

Playback experiments

We conducted 56 playback trials with 30 unique subjects, testing the hypothesis that Recruitment stimuli would be more likely than Display stimuli to induce resting subjects to move either towards or directly away from the source of the stimulus. In 21 matched pairs of trials ($N = 42$ total trials), the same subject heard both a Recruitment and a Display stimulus from the same stimulus pair. Paired trials were separated by a minimum of 3 full days and counterbalanced by order. An additional 14 trials (eight Recruitment trials, six Display trials) were unpaired. We knew the identity, age, sex and social rank of all focal subjects; all were adult natal clan members (≥ 24 months old) or immigrant males with tenures ≥ 6 months. Each subject heard calls of a clanmate, although none heard stimuli from a member of its own matriline.

To test the viability of the basic playback design, we conducted exploratory playback trials using unmanipulated whoop-bout recordings (not our subsequent experimental stimuli) recorded from one member of each clan. As in other playback studies on hyaenas (Benson-Amram et al., 2011; Holekamp et al., 1999), subjects' responses mirrored observed responses to naturally occurring distant whoops, ranging from apparent indifference in some trials to sustained attention in others. No subject showed any apparent inhibition of response due to the presence of either a nearby (observer) vehicle or a more distant (broadcast) vehicle. We therefore proceeded to experimental trials.

Playback experiments were conducted at dawn and dusk (0600–0900 hours; 1700–1900 hours) when hyaenas are active and there is sufficient light to record behaviour. We conducted playbacks only on solitary subjects (no other hyaenas visible within 500 m from either the subject or the broadcast vehicle) that were at rest (sitting or lying down) and not actively engaged in any activity that might compete with our stimuli for attention (e.g. feeding). All playbacks were conducted under weather conditions that allowed consistent sound transmission (neither in rain nor high wind). To control for the possible influence of extreme hunger or satiation, we scored potential subjects using an established four-point scale of body condition (1 = gaunt, 2 = normal, 3 = fat, 4 = obese) that reflects recent feeding behaviour (Watts & Holekamp, 2008) and carried out playbacks only with individuals in the two intermediate conditions (normal or fat).

In each trial, the stimulus bout was played only once and was broadcast from a research vehicle to which hyaenas were well habituated, parked 200 ± 10 m from the subject (distances determined by GPS with Garmin eTrex Legend and GPSMap 76 units, accurate to <4.5 m), in a location that would require the subject to visibly alter its baseline position (e.g. by raising or turning its head) in order to orient towards the sound. A second observer parked near the subject (15–30 m away) to cue the broadcast vehicle and to videotape subjects' responses.

We played stimulus bouts using the same configuration of audio equipment as that used for call-ins (see Part 1: Methods), with the exception that play volumes for each matched stimulus pair were set to maximum on the iPod and to a range of settings (25–40) on the Altec-Lansing speaker set, so as to equalize sound pressure levels across all stimuli at the same natural level (mean $\pm$ SE maximum pressure at 1 m = 109 ± 0.5 dB, measured with a Realistic Sound Level Meter, Radio Shack, Fort Worth, TX, U.S.A., accuracy ± 2 dB(A)). Playbacks sounded natural to human ears and subjects responded naturally as in the exploratory trials.

Subjects' responses were videorecorded from both cars. The observer car was equipped with a high-definition Canon Vixia HF200 camcorder to record detailed behaviour. Observers in the broadcast car used a GoPro Hero HD wide-angle portable camera to record the direction and pace of subjects that moved.

To control for subjects' behaviour immediately before playback, we videotaped all subjects for a 2 min baseline period before stimulus onset and continued videotaping after call onset for a standard minimum of 6 min. Filming then continued until the subject returned to a resting state for at least 10 s. The dependent variable for all trials was whether or not subjects moved from their original resting locations. Movements of less than 3 m were scored as 'orienting' responses but not as movement. We distinguished whether subjects moved towards or away from the speaker. For those trials in which subjects did move, a secondary dependent variable of interest was the latency to move (in seconds) after first orienting towards the stimulus. We also coded the direction of orientation, degree of postural arousal, direction and pace of movement. All playback trial videos were coded by A.S.G.; a subset of 20% of videos was coded by a second 'blind' observer. (All videos are available upon request.)

Ethical note

These experiments adhered to the ethical standards of the United States and Kenya, and all research was described in Animal Research Application number 05/14-087-00, approved most recently on 28 April 2014 by the Institutional Animal Care and Use Committee of Michigan State University.

Statistical analyses

We compared responses to Display and Recruitment stimuli using two generalized linear mixed models (GLMM). The first

GLMM used a binomial error structure to test the effects of the predictors on whether or not the subject moved after the stimulus ($N = 56$). For trials in which subjects did move ($N = 33$), we ran a second GLMM with a Poisson error distribution to test the effects of the predictors on a subject's latency to move after orienting towards the stimulus (see Results, Table 2). Individual callers and subjects appeared with different frequencies in the data set, so we included subject and caller ID as random factors in both models. The predictors were stimulus type (Display versus Recruitment), caller sex, trial number (1, 2), prey availability (high, low), rank disparity between caller and subject, body condition (normal, fat) and time of day (morning/evening). The second model also tested the predictor 'stimulus duration' for its possible influence on latency to move.

All statistical tests were performed, and all figures created, using R v. 3.0.2 (R Development Core Team, 2010). Mean values are given ± SE. We considered results significant when $P < 0.05$.

Results

Subjects' responses to display and recruitment playback stimuli

Subjects attended to playback stimuli across both stimulus conditions, spending significantly more time oriented towards the speaker during the 2 min after onset than during the 2 min of baseline in 54 of 56 trials (mean ± SE proportion time oriented to speaker: baseline: 0.04 ± 0.8; post-onset: 0.70 ± 0.29; $t_{53} = -16.9777$, $P < 0.001$), and adopting a more alert posture while orienting (by raising the head, sitting up, standing or some combination thereof) in 52 of 56 trials (29/29 Recruitment trials and 23/27 Display trials).

Although subjects in both Display and Recruitment trials attended to the playback stimulus, the two call types elicited different movement responses. Subjects moved in response to Recruitment stimuli in 22 of 29 trials, compared to 11 of 27 Display trials (Fig. 2). The full GLMM including all predictors was significantly better at predicting whether a subject moved than a null model including random factors only (likelihood ratio test: $\chi^2_8 = 26.11$, $P = 0.001$). Within the full model, stimulus type was

Table 1
Results of a GLMM analysis in which the dependent measure was whether subjects did or did not move in response to the playback stimulus

Predictor variables	β	SE	Z	P
(Intercept)	−6.411	3.745	−1.712	0.087
Stimulus type[a]	2.047	0.751	2.725	**0.006***
Trial number[b]	−1.120	0.841	−1.331	0.183
Natal/Immigrant subject[c]	2.070	1.248	1.659	**0.097†**
Caller sex[d]	−0.529	1.528	−0.346	0.729
Rank disparity[e]	0.038	0.047	0.812	0.417
Prey availability[f]	0.999	0.711	1.406	0.160
Body condition[g]	0.127	0.992	0.128	0.898
Time of day[h]	1.365	0.769	1.775	**0.076†**
Wind[i]	−0.120	0.544	−0.221	0.825

†$P < 0.1$; *$P < 0.01$. $N = 56$ trials.
[a] Stimulus type: Display or Recruitment.
[b] Trial number: 1 or 2 (for paired trials); 1 (for unpaired).
[c] Natal: adult females and undispersed males; immigrant: immigrant males.
[d] Caller sex: adult female or immigrant male.
[e] Rank disparity: caller's ordinal rank minus subject's ordinal rank, as determined using a matrix of outcomes of dyadic, agonistic interactions, including unsolicited appeasement behaviour (Smale et al., 1993) collected by all-occurrence sampling (Altmann, 1974) during daily observations.
[f] Availability: low or high, reflecting the presence or absence of large ungulate herds during migratory periods.
[g] Body condition: 1 = gaunt, 2 = normal, 3 = fat, 4 = obese; all subjects were either normal or fat.
[h] Time of day: morning or evening.
[i] Wind: 1 = none, 2 = light breeze, 3 = light–moderate wind.

Table 2
Results of a GLMM analysis in which the dependent measure was the latency of subjects to move after orienting to the playback stimulus

Predictor variables	β	SE	Z	P
(Intercept)	2.239	0.617	3.626	**<0.001****
Stimulus type	−0.012	0.177	−0.065	0.948
Stimulus duration (s)	0.007	0.005	1.476	0.140
Trial number	−0.106	0.152	−0.692	0.489
Caller sex	−0.253	0.206	−1.225	0.221
Rank disparity	0.010	0.005	1.979	**0.048***
Prey availability	0.251	0.129	1.939	**0.052†**
Body condition	−0.018	0.194	−0.093	0.926
Time of day	0.193	0.143	1.355	0.175
Wind	0.135	0.104	1.296	0.195

†$P < 0.1$; *$P < 0.05$; **$P < 0.001$. Effects for trials in which subject moved, excluding four outliers with unusually long latencies ($N = 29$). Definitions of predictor variables as in Table 1, with the exclusion of 'natal/immigrant' due to intercorrelation with rank disparity and the inclusion of stimulus duration.

the only variable that had a significant effect on whether the subject moved: subjects were significantly more likely to move after hearing Recruitment than Display stimuli ($P = 0.0064$; Table 1).

In trials that elicited movement directly towards or away from the speaker ($N = 33$), we frequently lost visual contact with subjects before they returned to a resting state. Fourteen such trials (42%) were curtailed when the subject entered terrain where observer cars could not follow, and in 10 such cases (30%) we lost visual contact with the subject before the end of the 6 min trial period. Additionally, in five of the 33 trials (15%), another hyaena, apparently responding to the playback stimulus, arrived on the scene and began interacting with the subject. We therefore restricted our statistical analyses to comparison of hyaenas' initial responses to playback stimuli.

Nevertheless, our observations suggest that once a hyaena initiated movement in response to a stimulus bout, that movement was persistent. For all trials in which we were able to track subjects for at least the full 6 min trial period ($N = 22$), the mean ± SE time spent travelling directly towards the speaker was 480 ± 60 s. The mean ± SE distance travelled in those trials was 487.2 ± 88.5 m.

Relationship between social rank and response latency

In the 33 trials in which subjects moved in response to the playback stimulus, movement began before the stimulus bout
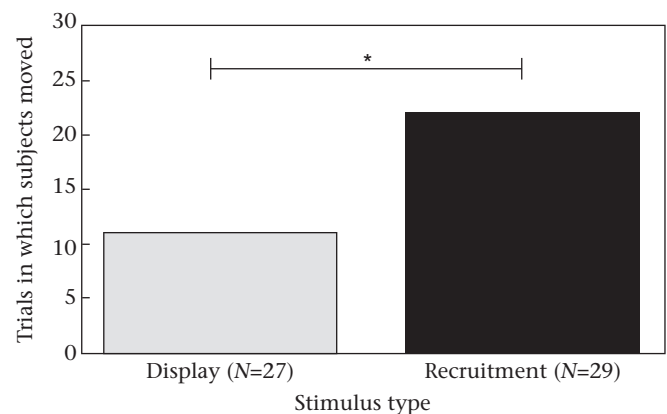

Figure 2. Numbers of trials in which subjects moved in response to hearing either a Display stimulus with lengthened inter-whoop intervals ($N = 27$ trials on 23 hyaenas) or a Recruitment stimulus with shortened intervals ($N = 29$ trials on 26 hyaenas). Subjects moved in 11/27 Display trials and 22/29 Recruitment trials. *$P < 0.01$; we assessed significance with a generalized linear mixed model, described in Table 1.

ended in the majority of cases ($N = 24$, 73%); in another five trials, subjects moved within 10 s of the end of the bout. There was considerable variation in latency to move (range 7–232 s). In the GLMM testing predictors' effects on latency to move, we dropped four long-latency outliers (latency to move = 96 s, 185 s, 206 s, 232 s; all outliers were higher-ranked individuals whose inclusion in the model enhanced the effects reported in Results), leaving 29 trials with latencies ranging from 7 to 41 s. The measures 'subject rank' and 'rank disparity' were highly intercorrelated ($r^2 = 0.87$); we retained the disparity measure because it captured both the subject's rank and its ordinal distance and hierarchical position (above or below) relative to the caller. Because the measure 'natal versus immigrant subject' was also highly correlated with rank disparity ($r^2 = 0.85$), we removed it from the list of predictors. Whereas stimulus type was the only significant predictor of subjects' movement, it did not predict their latency to move. However, the GLMM revealed a significant effect of rank disparity on subjects' latencies to move after orienting to the stimulus ($P = 0.048$; Table 2, Fig. 3): hyaenas were quicker to move when the stimulus came from callers that outranked them and slower to move when they outranked the caller. The full model including rank disparity fitted predicted latency times better than a null model including random factors only (likelihood ratio test: $\chi^2_9 = 35.76$, $P < 0.001$). The variable 'prey availability' also had an effect that approached significance ($P = 0.052$; Table 2), with subjects tending to respond more slowly in trials conducted when large, migratory herds were present in the study area. There was no interaction effect between prey availability and rank disparity ($P > 0.65$)

DISCUSSION

Hyaenas clearly demonstrated that they distinguished between Recruitment and Display stimuli based on one acoustic feature: the duration of inter-whoop intervals. Individuals moved significantly more often in response to Recruitment than to Display stimuli, and in all but three cases moved towards the source of the stimulus bouts. If these response rates reflect natural behaviour, hyaenas have an effective communicative tool for coordinating group defence.

Whereas stimulus type was the only significant predictor of subjects' movement, it did not predict subjects' latencies to move, which appeared to be influenced at least in part by the rank disparity between caller and recipient. Hyaenas were slower to move when they outranked the caller, and quicker to move when they were outranked. We might have expected rank disparities to produce the opposite trend, with hyaenas responding most strongly to whoops from lower-ranked callers from whom they could expect to successfully usurp food. Instead, the pattern we observed may reflect rank-dependent variation in the cost–benefit trade-offs associated with response times. Lower-ranked individuals lose food access as feeding group size grows (Smith et al., 2008), so responding quickly to a possible recruitment call could mean the difference between feeding as part of a small group and queuing at the bottom of a larger group. Because higher-ranked individuals join the feeding queue at the front, these individuals might be less intensely motivated to end a period of rest and invest in an extended search for the caller. Dramatic differences in the abundance of prey, as determined by the presence or absence of large migratory ungulate herds, may also have influenced response latencies. Like rank, recent prey abundance may have affected how well fed subjects were at the time of trials, or it may have influenced variation in individuals' expectations of either encountering or accessing food at the source of our Recruitment stimuli. The prey abundance ∗ rank disparity interaction term did not significantly
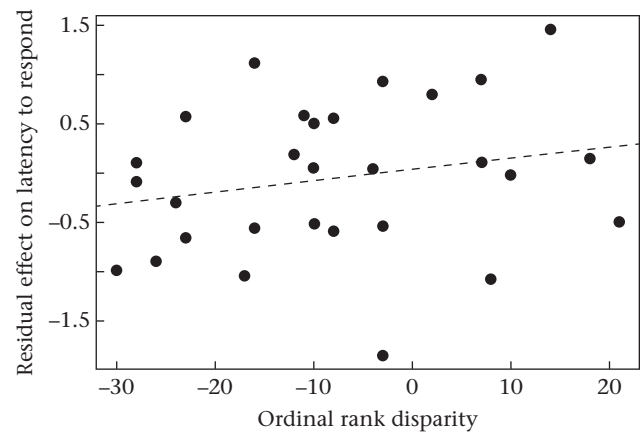
Figure 3. Residual plot showing the effect of ordinal rank disparity on subjects' latencies to move after orienting towards the stimulus (for all trials wherein subjects did move: 33 total trials with 4 outliers removed, $N = 29$). In trials with a negative rank disparity score, the subject's ordinal rank was lower than that of the calling hyaena; subjects that outranked the caller had positive rank disparity scores.

predict latency, perhaps because superabundant prey might have led all subjects to behave as only the highest-ranked hyaenas did when prey was more scarce. If satiety, or greater certainty of food access, slowed response times, this may have been a characteristic of high-ranked hyaenas throughout the year and of all hyaenas when migratory herds were present. Rank is stable over time but varies across individuals, while prey availability affects all clan members and varies over time.

The challenge of fission–fusion sociality is often presented as primarily cognitive, because members of such societies have to manage and respond appropriately to fitness-relevant social data without the reinforcement of frequent and predictable interactions (Amici, Aureli, & Call, 2008; Barrett, Henzi, & Dunbar, 2003). Whereas group instability may exert selective pressure on cognitive faculties to retain or manage information (Amici et al., 2008; Stevens & Gilby, 2004), communication systems may also evolve to bridge physical and temporal distances (Aureli et al., 2008). For spotted hyaenas, one challenge of fission–fusion sociality is that it regularly places group members far from the direct benefits of collective action. Hyaenas are compelled to range away from their groups to find food and escape conspecific aggression, but they may be equally constrained to converge and cooperate in the face of extragroup pressures. Hyaenas' ecology seems to demand collective defence behaviour, and the circumstances under which that behaviour must be coordinated appear to require signals that effectively support cooperation across dispersed networks.

We found that modifying just one aspect of whoop bouts (the duration of the inter-whoop interval) resulted in a signal that attracted listeners despite variation in their motivational states and despite the absence of visual or other contextual cues. The repetitive structure of this vocalization seems to be relevant: To determine the nature of an ambiguous signal, such as a whoop bout that might function either as a display or a recruitment call, listeners close to the signaller can collect data from other sources in the environment. The greater the distance between caller and receiver, the sparser these supporting data will become, but redundancy in the signal itself may be a way to compensate. During real lion–hyaena conflicts, some hyaenas may be able to hear the concurrent sounds of whoops and lion roars, smell blood, or see other clan members running towards the conflict. However, our results suggest these contextual cues are not required for hyaenas to communicate effectively. In contrast to this sensorially rich scenario, our experiments offered subjects just one whoop bout,

but each successive whoop and interval may have provided increased certainty about the nature of the call. Bouts, then, may be a structural adaptation that conforms to findings from research on the informational value of redundancy within multimodal and multicomponent signals in a variety of species (Chittka, Dyer, Bock, & Dornhaus, 2003; Ernst & Banks, 2002; Gepshtein & Banks, 2003; Kulahci, Dornhaus, & Papaj, 2008; Roach, Heron, & McGraw, 2006; Van Beers, Wolpert, & Haggard, 2002). Additionally, there is a great deal of structural variation across whoops and bouts that this study leaves unexplored. Variation in other parameters may contribute additional information to the distinction between display and recruitment bouts, or even to other functions of this call. Although the concept of information remains somewhat controversial in the animal-signalling literature (Rendall, Owren, & Ryan, 2009; Scott-Phillips, 2008; Seyfarth et al., 2010; Townsend & Manser, 2013; Wheeler & Fischer, 2012), it seems unlikely that hyaenas' recruitment calls would induce receivers to approach callers from long distances if they did not create some kind of 'informed' expectation in receivers. Considering the intense competition between hyaenas and lions, individual hyaenas probably could not afford to range as widely as they do if they did not possess an effective long-distance recruitment signal. Thus, the features that make whoops effective in different functional contexts, the vocal apparatus that amplifies long-distance whoops, and the social structure that requires them, may all have imposed direct evolutionary constraints on one another.

Acknowledgments

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