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Numerical assessment and individual call discrimination by wild spotted hyaenas, *Crocuta crocuta*

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Game theory predicts that individuals should assess numbers of potential opponents before engaging in aggressive interactions, particularly when numerical odds can determine outcomes of such interactions. Spotted hyaenas, *Crocuta crocuta*, live in fission–fusion societies in which extreme numerical imbalances can occur during intergroup conflicts, which are potentially lethal. Thus, an ability to assess relative numbers of opponents should be highly advantageous in this species. Here we tested abilities of wild spotted hyaenas to assess numerical advantage with a playback experiment by presenting contact calls produced by one, two or three unknown hyaenas, or ‘intruders’, to individuals in our study clans. Hyaenas conformed to predictions of game theory by increasing vigilance to playbacks of multiple unfamiliar intruders. Furthermore, hyaenas distinguished not just between calls produced by one versus multiple intruders, but showed a fine-grained ability to assess numerical advantage, and they responded with increasing levels of vigilance to calls produced by one, two and three unknown intruders. Hyaenas also took more risks by approaching the speaker when they outnumbered calling intruders. Lastly, this study provides experimental evidence that spotted hyaenas can use contact calls to distinguish among individuals.

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Game theory predicts that animals should assess the strength and relative numbers of potential opponents before engaging in aggressive interactions (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Maynard Smith 1982). The ability to assess numerical advantage should be prevalent in species with intergroup conflicts, particularly those living in fission–fusion societies (Manson & Wrangham 1991; Wrangham 1999; Hauser 2001). Fission–fusion societies are stable social units in which individual group members are often found alone or in small subgroups and in which subgroup size and composition change frequently over time. Numerical imbalances may thus be more extreme in fission–fusion societies than in more cohesive social units. This variation in subgroup size may lead to higher intergroup aggression, involving potentially lethal attacks, because numerically superior subgroups can attack at relatively low cost to themselves (Manson & Wrangham 1991). Such conditions can therefore be expected to increase selection for the ability to assess numerical odds, or the ratio of number of defenders to number of intruders, in order to gauge the costs of engaging in aggressive intergroup interactions.

Previous playback experiments showed that wild lions, *Panthera leo*, and chimpanzees, *Pan troglodytes*, both of which live in

fission–fusion societies, spontaneously demonstrate rudimentary abilities to assess numerical advantage. Lions were able to distinguish between one and three foreign conspecifics, and they responded more aggressively when faced with fewer intruders and when their own group size was relatively large (McComb et al. 1994). Lone adult male lions were also slower to approach the sound source when hearing roars produced by three unknown males within their territory than when hearing roars produced by just one male (Grinnell et al. 1995). Similarly, chimpanzees varied their responses to calls produced by a single foreign male in their territory based on the number of male group members present in the listeners’ party (Wilson et al. 2001); parties with three or more males consistently vocalized and approached the sound source whereas parties with fewer males stayed silent and rarely approached. Thus, both lions and chimpanzees adjust their responses to calls produced by foreign intruders based on numerical odds.

We conducted playback experiments to test the hypothesis that wild spotted hyaenas can assess numerical advantage when hearing calls produced by one, two or three foreign intruders. Similar to lions and chimpanzees, spotted hyaenas live in fission–fusion social groups, called clans, which contain up to 90 individuals that cooperate to defend a group territory (Henschel & Skinner 1991; Holekamp et al. 1997a, b; Boydston et al. 2001). In addition, spotted hyaenas, lions and chimpanzees all have potentially lethal intergroup conflicts in which numerical advantage often determines outcomes (Kruuk 1972; Kruuk & Macdonald 1985; Packer et al. 1990;

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Wrangham 1999; Wilson et al. 2002). Given the similarities among these species, we predicted that hyaenas would demonstrate an ability to assess numerical advantage comparable to that demonstrated by lions and chimpanzees. Based on predictions of game theory that contest asymmetries can determine outcomes (Maynard Smith 1979) and that individuals should be more willing to engage in contests when the benefits outweigh the costs (Wilson et al. 2001), we predicted that hyaenas would take the greatest risks when they encountered the best numerical odds, and that they would be most cautious when confronting the worst numerical odds.

We used sound stimuli produced by one, two and three intruders to test whether hyaenas can discriminate among various numbers of calling individuals. A variety of birds and mammals can discriminate among specific numbers of physical objects (Capaldi & Miller 1988; Brannon & Terrace 1998; Lyon 2003; Pepperberg 2006). However, we know little about the precision of animals' discrimination abilities when presented with variable numbers of acoustic stimuli. The ability of hyaenas to distinguish precisely among one, two, or three different voices would indicate that they can discriminate among, and keep track of, calls produced by individual conspecifics. Individual discrimination based on vocalizations may be obligatory for arboreal species because group members are often out of sight of one another (Ghazanfar & Santos 2004). The same logic may apply in species with fission–fusion societies, in which group members are often separated. We thus predicted that spotted hyaenas would discriminate among individuals based on their calls.

We also tested whether hyaenas show individual differences in their responses to calls produced by unknown intruders. If hyaenas respond solely based on numerical odds, individuals should not vary significantly from other hyaenas in how they respond to each treatment. However, hyaenas may show significant variation among individuals if traits such as social rank also influence their responses. For example, the benefits of territorial defence and participation in intergroup contests may vary among individual group members, and individuals might modify their participation based on the benefits they are expected to receive (Nunn 2000; Kitchen 2004, 2006; Kitchen & Beehner 2007). Earlier work with lions (Heinsohn & Packer 1995) and black howler monkeys, *Alouatta pigra* (Kitchen 2006), revealed marked variation among individuals in their responses to simulated intruders. Spotted hyaena societies are rigidly structured by linear dominance hierarchies in which an individual's social rank determines its priority of access to food. Because food intake affects reproductive output among females, high-ranking females enjoy greater reproductive success and offspring survival than lower-ranking females (Holekamp et al. 1996; Hofer & East 2003). If differential food access within the territory affects the value of the territory for adult female hyaenas, high-ranking females should take more risks when hearing calls produced by territorial intruders, whereas low-ranking females should respond more cautiously and engage in fewer risky or aggressive behaviours. We tested whether individual adult females varied in their responses to calls produced by variable numbers of intruders, and whether responses could be predicted by social rank.

METHODS

Subjects and Study Site

We conducted playback experiments on members of two spotted hyaena clans in the Masai Mara National Reserve (henceforth 'Mara') in southwestern Kenya. We collected data for this study from July 2007 to May 2008, and throughout this period we monitored the study clans daily during 0530–0900 and 1700–2000 hours. We determined territorial borders for the two study clans following methods from Boydston et al. (2001).

We identified individuals by their unique spots and other natural markings. We determined sex from the dimorphic shape of the glans of the erect phallus (Frank 1990). We estimated age to ± 7 days for all individuals born in both study clans, as described by Holekamp et al. (1996). We considered hyaenas to be juveniles up to 24 months of age, and adults when they were older than 24 months. We used all-occurrence sampling (Altmann 1974) to determine the social rank of each adult based on its position in a matrix of outcomes of dyadic, agonistic interactions, including unsolicited appeasements (Holekamp & Smale 1990; Smale et al. 1993).

Acoustic Stimuli

We used spotted hyaena whoop vocalizations as acoustic stimuli; each vocalization is a series of discrete calls that together form a whoop bout. Whoops are produced by both male and female hyaenas of all ages, and function as long-distance contact calls (Kruuk 1972; East & Hofer 1991). To ensure that stimulus whoops were produced by individuals unknown to hyaenas in our study clans, we obtained whoops recorded in Tanzania, Malawi and Senegal from the British Library. We obtained six different stimulus whoop bouts of high acoustic quality, all from the only extant subspecies of spotted hyaenas. The British Library provided no information regarding the age, sex or identity of the hyaenas that produced these whoop bouts. Therefore, it is possible that the same individual may have produced more than one of these calls. However, this seems highly unlikely, particularly because the whoop bouts recorded from single individuals in Tanzania and Malawi appear to be more similar to one another than the four whoop bouts recorded from individuals in Senegal (Fig. 1). In addition, previous research suggests that the structure and number of harmonics in whoops vary among individuals (East & Hofer 1991), and visual inspection of spectrograms of the whoop bouts from each caller revealed substantial variation (Fig. 1).

It is also possible that hyaenas would respond to the playbacks based on the age or sex of the caller. Minimum fundamental frequency is a major acoustic characteristic distinguishing whoops of callers from different age and sex classes (Theis et al. 2007). Although minimum fundamental frequency varied among our stimulus whoops (Table 1), with the possible exception of whoop bout C, all whoops fell within the adult range (Theis et al. 2007). Juvenile whoops contain fewer and more widely spaced harmonics than adult whoops (East & Hofer 1991), yet bout C has more harmonics than the other bouts, so it is likely that all the stimulus whoops were produced by adults. Nevertheless, we examined the acoustic properties of each whoop bout in detail (Table 1), and we incorporated variation in acoustic variables into our statistical analyses. We also included caller ID as a covariate in our analyses of behavioural responses to these stimuli (see Statistical Analyses).

Whoop vocalizations have acoustic properties that vary with call context and influence conspecific responses (Theis et al. 2007). To control for these effects, we constructed stimulus whoop bouts in which all interwhoop intervals were 2 s long. We also controlled for the number of calls per bout despite no evidence that this measure varies with call context or affects conspecific responses (Theis et al. 2007). The mean \pm SE number of calls per bout was 9 ± 1.36 in the stimulus whoop bouts from the British Library, so we constructed bouts with nine calls to minimize manipulation of the sound stimuli. To do so, we removed or added calls as necessary, randomly using calls from the middle portion of the bout to avoid removing terminal calls, which often have a different structure (East & Hofer 1991; Theis et al. 2007). We edited all stimulus whoop bouts using Raven (Charif et al. 2004) and Praat (Boersma & Weenink 2004) software, and applied a filter function in Raven (Charif et al. 2004) to remove background noise.

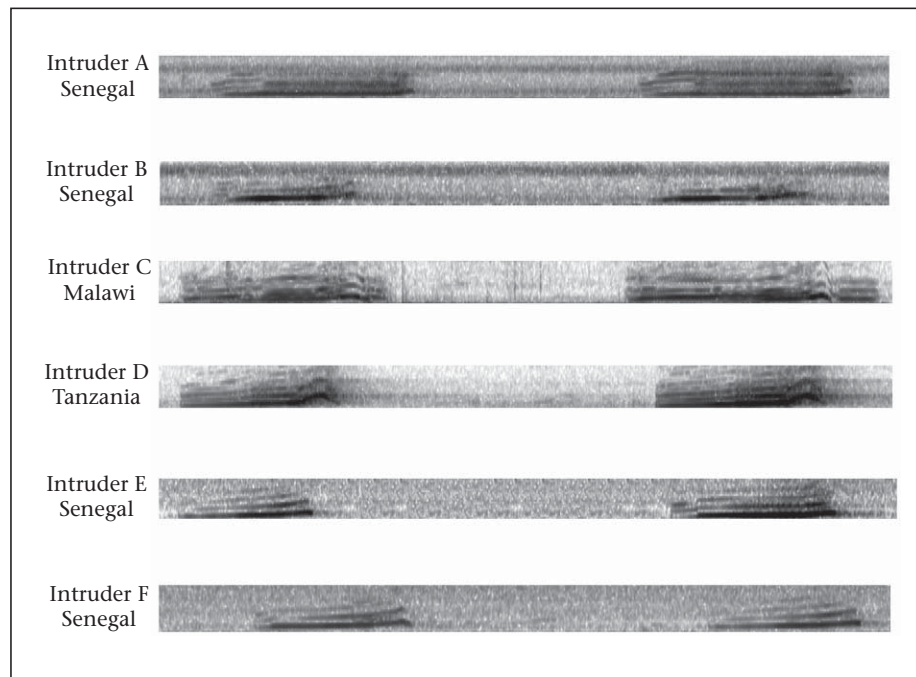


Figure 1. Spectrograms showing the structure of two whoop calls within a bout from each stimulus sound. For each caller, two individual whoops are shown, separated by an interwhoop interval. All spectrograms have the same frequency scale of 0–2 kHz.

Stimulus Configuration

The playback of whoops produced by foreign hyaenas simulated intruders in the territories of our subject hyaenas. To avoid confounding stimulus intensity with the number of callers (Hauser 2001), we conducted playback experiments using consecutive and nonoverlapping calls as test stimuli. To control stimulus duration, we played each focal hyaena three consecutive whoop bouts, varying the identities of the callers but not the number of whoop bouts heard. There were three treatment conditions, each of which featured whoop bouts produced by one, two, or three different intruders. In the 1-intruder treatment we repeated a whoop bout produced by one individual three times. The 2-intruder treatment began with a whoop bout produced by one individual, followed by a whoop bout produced by a different individual, followed by a whoop bout produced by either the first or second individual. The 3-intruder treatment presented whoop bouts produced by three different individuals.

The order in which individuals were exposed to the three different treatments was randomized. The particular sound stimulus played was also essentially random, although we attempted to avoid playing the same calls to subjects multiple times. We used five stimulus

configurations as sound stimuli for the 1-intruder treatment, six configurations for the 2-intruder treatment, and two configurations for the 3-intruder treatment. Stimulus configurations were used in an average \pm SE of 3 ± 0.58 trials and individual hyaenas heard each stimulus recording in an average \pm SE of 1.19 ± 0.019 trials. Individual hyaenas heard a specific recording no more than two times during the 11-month study period. Hyaenas were involved, either as a focal subject or as an arriving individual during group trials, in an average \pm SE of 1.94 ± 0.20 trials (range 1–5 trials). To reduce habituation to playback stimuli, we separated playbacks to any individual by at least 7 days, and the mean \pm SE time between trials within individuals was 52.39 ± 9.17 days.

Playback Set-up

We conducted playbacks around dawn and dusk (0600–0900 and 1730–1900 hours) when wind was negligible, hyaenas were active and ambient lighting conditions permitted high-quality data collection. We conducted playbacks near the centre of the focal hyaena's territory to increase the likelihood that the hyaena would view the unfamiliar calls as coming from intruders. In addition, we

Table 1
Acoustic properties of stimulus whoops assessed in the present study

ID	Location	Min. fund. freq. (Hz)	Peak fund. freq. (Hz)	Whoop dur. (s)	Bout dur. (s)	RMS amp.*	Max amp.*	Max freq. (Hz)	Max power (dB)	No. of harmonics
A	Senegal	264.48 \pm 4.88	443.34 \pm 9.86	2.01 \pm 0.16	36.81	2531.46 \pm 59.29	8158.11 \pm 254.79	354.08 \pm 9.58	117.40 \pm 0.25	4
B	Senegal	255.86 \pm 7.35	481.13 \pm 25.14	1.2 \pm 0.06	29.25	2078.84 \pm 156.71	6448.56 \pm 334.77	333.39 \pm 11.11	115.97 \pm 0.58	3.1 \pm 0.20
C	Malawi	320.60 \pm 10.36	509.87 \pm 13.49	1.86 \pm 0.07	34.76	1908.46 \pm 115.22	7860.22 \pm 491.58	448.72 \pm 12.91	115.81 \pm 0.84	5.4 \pm 0.29
D	Tanzania	195.67 \pm 4.37	703.57 \pm 10.55	1.22 \pm 0.03	29.64	2623.56 \pm 363.31	11611 \pm 1374.76	373.23 \pm 14.36	121.03 \pm 0.93	3.4 \pm 0.18
E	Senegal	285.90 \pm 4.94	469.87 \pm 15.87	1.29 \pm 0.12	30.97	2959.27 \pm 459.42	8758.78 \pm 1175.9	373.23 \pm 14.36	117.56 \pm 1.46	3.8 \pm 0.15
F	Senegal	274.34 \pm 2.83	471.74 \pm 25.67	1.40 \pm 0.08	30.7	1474.20 \pm 159.46	5668.33 \pm 519.24	382.81 \pm 15.14	112.19 \pm 1.04	3.5 \pm 0.18
GLM†		$F_{5,48}=43.09$, $P<0.0001$	$F_{5,48}=28.4$, $P<0.0001$	$F_{5,48}=21.4$, $P<0.0001$		$F_{5,48}=4.30$, $P=0.0026$	$F_{5,48}=6.50$, $P=0.0001$	$F_{5,48}=8.94$, $P<0.0001$	$F_{5,48}=9.62$, $P<0.0001$	$F_{5,48}=19.2$, $P<0.0001$

All measurements are means \pm SE of all whoops within a bout, except for bout duration, which is the mean \pm SE duration of a bout of nine whoops.

* RMS (root-mean-square) amplitude and maximum amplitude are measured in dimensionless sampling units, for more information see Charif et al. (2004).

† GLMs were conducted for each measure to compare overall variation among test stimuli.

conducted playbacks at least 250 m from active communal den sites.

Sex, age and social rank were known for each playback subject. We scored the body condition of each individual from 1 (thinnest) to 4 (fattest) using a previously established scale that reflects recent food consumption (Watts & Holekamp 2008). To minimize variation in response due to motivation or hunger, we only conducted trials when individuals were in the two intermediate body conditions (normal or fat) and not when they were in the extreme body conditions (gaunt or obese).

We played whoop bouts from an iPod mounted in a concealed BOSE portable SoundDock; sound stimuli were broadcast from a research vehicle to which the hyaenas were well habituated. Following methods used by Watts et al. (2010), we broadcast sounds 95.95 ± 1.60 m (mean \pm SE) from the focal hyaena(s). We measured distance from the focal individual(s) to the speaker at sound onset and again at sound offset using a Bushnell Yardage Pro Sport laser range finder. All sound stimuli were played at maximum volume, and at natural sound pressure levels (mean \pm SE maximum pressure at 1 m = 109 ± 0.5 dB, measured with a Digital Sound Level Meter manufactured by Radio Shack set at a C-weighting). The playbacks broadcast natural to our ears, and the hyaenas responded to the broadcasts, as described below. Our methods follow those used in earlier playback experiments on hyaenas and olive baboons, *Papio hamadryas anubis* (Lemasson et al. 2008; Watts et al. 2010).

Data Extraction from Videotaped Playbacks

We videotaped focal hyaenas during the 3 min before sound onset and throughout the 'response period', which started at sound onset and lasted for at least 3 min after the sound stimulus ended. The duration of the sound stimulus (mean = 95.11 s, range 87–110 s) made it possible for the focal hyaenas to assess the information presented to them by the callers while the sound was playing. We thus divided the response period into two intervals: (1) the 'playback period', during which the sound stimulus was playing, and (2) the remainder of the trial after sound offset.

We extracted the following behavioural measures from each videotaped playback trial: time orienting towards the speaker, response duration, latency to travel, direction of travel, distance moved and any instances of focal hyaenas vocalizing. A hyaena was orienting when its head was off the ground and facing the speaker, such that both ears were visible to the observer in the research vehicle. We defined response duration as the time from when a hyaena first changed its behaviour after sound onset until it ceased responding to the sound, or until the hyaena went out of sight, whichever occurred first. A hyaena that never altered its behaviour during the playback trial was assigned a response duration of zero. We defined latency to travel as the time from sound onset until the focal hyaena began moving. A hyaena that failed to travel was assigned a latency of 3 min; failure to orient was handled in the same fashion. We recorded direction of travel as either approaching the speaker by moving towards it, or avoiding the speaker by moving away from it. Distance moved was the distance in metres that a focal hyaena travelled from its starting position relative to the location of the speaker. In addition to the above measures, we also recorded the identity, age, sex and time of arrival for all hyaenas that arrived at the playback location after sound onset. S.B.A., V.K.H. and S.L.D. extracted data, and interobserver reliability was $r = 0.98$ or higher.

Sample Size

We conducted 39 playback trials: 35 to 12 lone adult female subjects and four to groups of adult hyaenas. For nine adult

females, we obtained matched samples in all three treatments when the subjects were alone. All trials to lone adult females started with an initial group size of one. In six of the 35 playbacks to lone adult females, conspecifics arrived at the playback location after sound onset and these trials had final group sizes greater than one. We therefore had 10 trials with final group sizes greater than one.

In our analyses of orienting behaviour, our sample size was 34 trials. We excluded one trial on a lone hyaena because several hyaenas arrived while the sound stimulus was playing, which altered the focal hyaena's orienting behaviour. However, we included orienting data from the other five trials, in which conspecifics arrived at the playback location after sound stimulus offset. We could not extract orienting data for playbacks to groups due to inadequate video quality resulting from the wide angle needed to keep all group members on the screen at all times.

Statistical Analyses

Responses by lone hyaenas to variable numbers of intruders

We compared the proportion of time lone hyaenas spent orienting towards the speaker before sound onset and during the playback period when hearing the calls of one versus multiple intruders. We used generalized linear mixed models (GLMM), with proportion of time spent orienting as the continuous response variable and the following fixed predictor variables: period (either the 3 min preplayback period, or the playback period), intruder number (one versus multiple), and the interaction between period and intruder number. For response variables that only occurred in the period after sound onset (distance moved, response duration and latency to travel), intruder number was the only fixed predictor variable. To control for pseudoreplication, focal hyaena identity (ID) was included as a random effect in all models.

We examined the abilities of hyaenas to differentiate among calls produced by one, two and three intruders by comparing orienting behaviour of lone hyaenas across the three treatments. We only included orienting behaviour in this analysis because very few lone hyaenas moved after sound onset. For clarity, we refer to the 1-, 2- and 3-intruder treatments as T1, T2 and T3, respectively, and we refer to the first, second and third whoop bouts within each treatment with numerical subscripts. We compared orienting behaviour during each round of whoop bouts across all three treatment conditions (e.g. T1₁ versus T2₁ versus T3₁) using a GLMM with proportion of time spent orienting during each whoop bout as a continuous response variable and with whoop bout duration and number of intruders as fixed predictor variables.

We next determined how the orienting behaviour of lone hyaenas within each treatment condition changed as they heard each successive whoop bout (e.g. T1₁ versus T1₂ versus T1₃). We used a GLMM with proportion of time spent orienting as the continuous response variable, and with whoop bout duration, whoop bout number and trial number as fixed predictor variables. Trial number was included as a predictor to determine whether hyaenas were habituating to the playback stimuli in later trials. Our sample sizes for each treatment condition were 12 trials for T1, 12 trials for T2 and 10 trials for T3.

Individual differences in vigilance

To investigate individual variability in orienting responses across all trials, we used only the nine adult females for which we had matched samples across all three treatments. We used a likelihood ratio test to compare generalized linear models (GLM) with and without the ID of the focal hyaena as a random effect. We also included social rank of the focal hyaena as a covariate in the model.

Influence of intruder identity

We examined variation in the acoustic properties of the stimulus whoop bouts using GLM with the acoustic property of interest as the continuous response variable and intruder ID as a fixed predictor variable. The acoustic properties and their measurements are listed in Table 1. We then investigated whether the identity of the intruder influenced variation in orienting responses among lone hyaenas. We examined responses to the first whoop bout across all treatment conditions, because these responses were expected to be the same. We used a likelihood ratio test to compare models with and without the ID of the intruder as a random effect. We then added each acoustic property as a fixed covariate to determine whether the magnitude of the random effect would decrease and would therefore show which acoustic properties were causing variation in orienting responses.

Effect of listener group size

We next examined the effects of listener group size and numerical odds on the probability that hyaenas would approach the speaker. We focused on approach behaviour in group trials because orienting behaviour could not reliably be extracted for all individuals present in group trials. To avoid pseudoreplication, each group trial was assigned only one response value per analysis. We scored each group as 'approaching the speaker' when over 50% of the individuals present in a trial decreased their distance to the speaker. We performed a logistic regression with approach (Y/N) as the binomial response variable, arrivals (Y/N) as a binomial fixed effect, ID of the focal hyaena as a random effect, and final group size, numerical odds at the end of the trial and rank of the focal hyaena as continuous fixed effects. We separated highly correlated predictor variables into different models, and alternative models were compared using Akaike's Information Criterion (AICc) values corrected for low sample sizes. A smaller AICc value indicated a better-fitting model (Crawley 2007).

We conducted all GLM, GLMM, logistic regressions and likelihood ratio tests in R 2.6.2 (R Development Core Team 2006). Mean values are given \pm SE. We considered results significant when $P < 0.05$.

RESULTS

Responses by Lone Hyaenas to Variable Numbers of Intruders

In all treatments, lone females spent a greater proportion of time orienting towards the speaker after sound onset than during the 3 min prior to sound onset ($t_{53} = -10.35$, $P < 0.0001$; Fig. 2). Lone hyaenas also spent significantly more time orienting towards the speaker when hearing the calls of multiple intruders than when hearing the call of a single intruder ($t_{53} = -3.04$, $P = 0.004$; Fig. 2). The interaction between playback period and intruder number was also significant ($F_{1,53} = 5.53$, $P = 0.022$), showing that responses of focal hyaenas to the playback depended upon the number of hyaenas calling in the sound stimulus. Too few hyaenas continued to orient during the 3 min period after sound offset to include those data in our analyses.

Lone hyaenas varied in their orienting responses to calls produced by one, two and three intruders. We expected that hyaenas in all three treatments would respond similarly to the first whoop bout because the first whoop bout of every trial was produced by a single unknown intruder. As expected, hyaenas showed the same orienting response to the first whoop bout, regardless of treatment condition ($F_{2,20} = 1.87$, $P = 0.18$; Fig. 3). Focal hyaenas then changed their orienting behaviour after hearing the first whoop bout, depending on the sound stimuli they heard during the remainder of the playback trial. The grey bars in Fig. 3 show that hyaenas in the 1- and 2-intruder treatments responded differently to the second whoop bout (T1₂ versus T2₂: $t_{19} = 2.59$, $P = 0.018$). Hyaenas in the 2-intruder

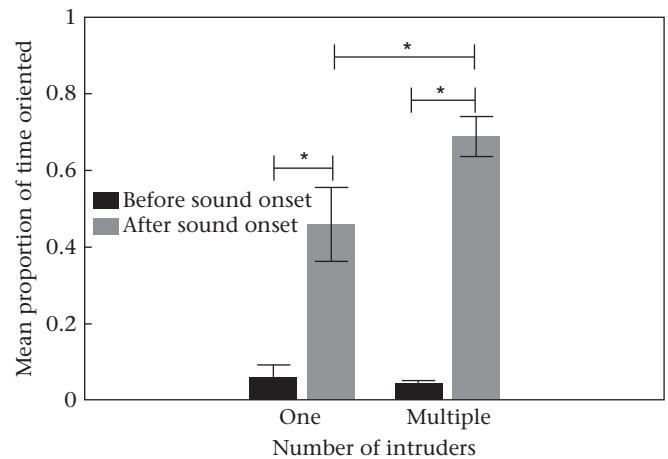


Figure 2. Mean \pm SE proportion of time spent oriented towards the speaker in 34 trials with 12 lone hyaenas during the 3 min before and after sound onset of playbacks of whoops from one intruder ($N = 12$ trials on 11 hyaenas) or multiple intruders ($N = 22$ trials on 11 hyaenas). * $P < 0.05$.

treatment oriented longer to the speaker than those in the 1-intruder treatment, most likely because they heard a whoop bout produced by an intruder they had not heard previously, whereas those in the 1-intruder treatment heard the same whoop bout as before. Likewise, the white bars in Fig. 3 show that hyaenas in the 1-intruder treatment spent significantly less time oriented towards the speaker than hyaenas in the 3-intruder treatment during the third whoop bout (T1₃ versus T3₃: $t_{19} = 2.27$, $P = 0.035$).

Hyaenas' orienting responses demonstrated that they distinguished between whoops they had heard before and whoops to which they had not previously been exposed. Specifically, hyaenas became less vigilant and spent less time oriented towards the speaker when they heard repeated whoop bouts produced by the same individual, even when whoops were not produced consecutively (T1₁ versus T1₃: $t_{22} = -2.49$, $P = 0.021$; T2₂ versus T2₃: $t_{21} = -2.27$, $P = 0.034$; Fig. 3); hyaenas increased vigilance levels and time spent oriented only when they heard a new whoop bout that indicated an unfamiliar individual (T3₁ versus T3₂: $t_{17} = 2.17$, $P = 0.045$; T3₁ versus T3₃: $t_{17} = 3.29$, $P = 0.0043$).

Trial number was not a significant predictor of orienting behaviour ($F_{3,7} = 0.16$, $P = 0.92$), demonstrating that hyaenas did not habituate to the playback stimuli in later trials. Furthermore, hyaenas did not show signs of habituation across whoop bouts within a trial because rather than diminishing responses in all our treatments, as would be expected during habituation, our subjects' responses intensified when they heard new voices in second or third bouts.

Focal hyaenas vocalized in only three playback trials and, therefore, we were unable to examine statistically vocalizing as a response variable. However, the three instances of vocalizing occurred in response to three different stimulus configurations and were produced by three different subjects. Thus, we saw no indication that a particular treatment or recording elicited vocalizations, or that any individual focal hyaena vocalized more than others. We also saw no effect of treatment condition on response duration among lone hyaenas ($F_{2,20} = 0.58$, $P = 0.57$). This finding is likely because significant orienting differences across treatments during the playback period were mitigated by a lack of orienting differences, and differences in other response variables included in this metric, across treatments once the playback period ended. We also found no effect of treatment condition on latency to travel ($F_{2,20} = 0.27$, $P = 0.77$) or distance moved ($F_{2,20} = 1.25$, $P = 0.31$) in trials involving lone hyaenas. Hyaenas that did approach the speaker usually waited until the sound stimulus ended, or until they heard a whoop bout

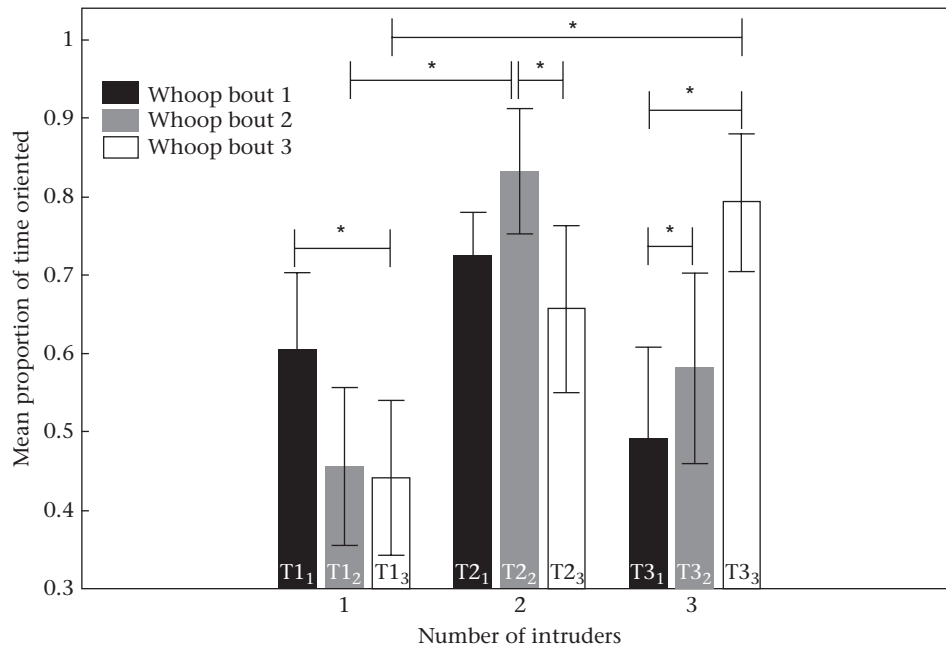


Figure 3. Mean \pm SE proportion of time spent oriented towards the speaker in 34 trials with 12 lone hyaenas during each whoop bout when hearing calls from one intruder ($N = 12$ trials on 11 hyaenas), two intruders ($N = 12$ trials on 10 hyaenas), or three intruders ($N = 10$ trials on 10 hyaenas). T1, T2 and T3 refer to the 1-, 2- and 3-intruder treatments, respectively, and the numerical subscripts refer to the first, second and third whoop bouts within each treatment. * $P < 0.05$.

repeated (in the 1- and 2-intruder treatments), before moving from their starting position (mean latency to travel = 146.89 ± 61.54 s).

Individual Differences in Vigilance

Individual hyaenas varied in their orienting behaviour across treatment conditions, with some individuals showing higher overall vigilance than others (likelihood ratio test: $\chi^2_1 = 50.55$, $P < 0.0001$; Fig. 4). Social rank was not a significant predictor of the mean proportion of time spent orienting ($F_{1,7} = 0.30$, $P = 0.60$). Some adult females showed high levels of variability in orienting

behaviour across all treatments (hyaenas with large standard errors in Fig. 4), but we also found relatively low variance in roughly half of the adult females (hyaenas with small standard errors in Fig. 4). Interestingly, females with low variance tended to be highly vigilant, on average.

Influence of Intruder Identity

Given that we found significant variation among intruders in the acoustic properties of their whoop calls (see Table 1), we inquired whether the identity of the intruder influenced orienting responses

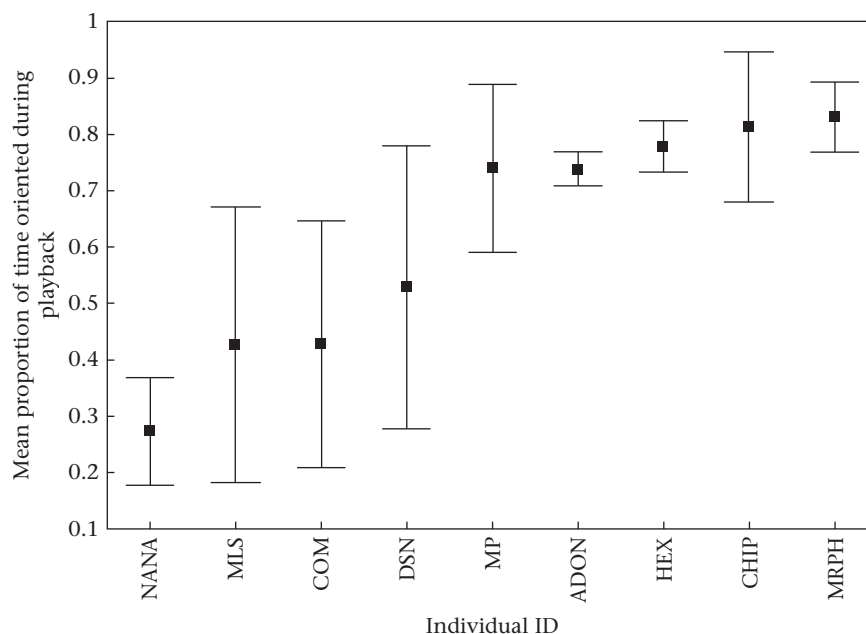


Figure 4. Mean \pm SE proportion of time spent oriented during the playback period across all three treatment conditions for each individual hyaena. Only adult females that experienced all three treatment conditions when alone ($N = 9$) were included.

Table 2

Summary of model comparison results investigating approach behaviour as a function of group size and numerical odds

Model	Predictor	Estimate	SE	Z	P	AICc
1	Final group size (continuous)	1.14	0.43	2.68	0.008	42.97
1b	Final group size group=1 vs group>1	2.42	0.85	2.85	0.004	45.57
1c	Final group size group<3 vs group≥3	2.53	0.93	2.7	0.006	46.15
2	Arriving individual	3.57	1.29	2.77	0.006	45.93
3	Final group size	0.98	0.50	1.97	0.048	43.4
	Arriving individual	2.25	1.48	1.52	0.13	
4	Numerical odds (continuous)	0.96	0.62	1.54	0.12	50.41
4b	Numerical odds, odds>1 vs odds≤1	2.92	1.17	2.48	0.013	46.2
Nonsignificant predictors		df	Log likelihood	χ^2	P	AICc
Rank of focal hyaena		3	-23.38	1.39	0.24	52.76
Number of intruders heard		4	-23.33	1.48	0.48	54.67

among lone hyaenas. A likelihood ratio test revealed a significant difference in time spent orienting between linear mixed effect models with and without intruder ID as a random effect ($\chi^2_1 = 5.47$, $P = 0.019$). To determine which acoustic properties were responsible for this effect of intruder ID, we added each acoustic property to the model individually, and found that the addition of whoop duration, bout duration or RMS amplitude as a covariate eliminated the effect of intruder ID (whoop duration: $\chi^2_1 = 0.57$, $P = 0.45$; bout duration: $\chi^2_1 = 1.29$, $P = 0.26$; RMS amplitude: $\chi^2_1 = 0.28$, $P = 0.59$). RMS amplitude is defined as the root-mean-square, or 'effective' amplitude, which is calculated by taking the square-root of the mean of the square of all instantaneous amplitude values of the call (Charif et al. 2004). Bout duration is a consequence of differences in whoop duration when interwhoop intervals are equalized, so these are effectively equivalent acoustic properties. Controlling for bout duration eliminated the significant effect of Intruder ID, demonstrating that hyaenas oriented longer when hearing longer calls. Adding other acoustic properties had no effect on the significance of intruder ID as a random effect (minimum fundamental frequency: $\chi^2_1 = 4.27$, $P = 0.04$; peak frequency: $\chi^2_1 = 4.07$, $P = 0.04$; maximum frequency: $\chi^2_1 = 5.18$, $P = 0.02$; maximum amplitude: $\chi^2_1 = 3.95$, $P = 0.04$; power: $\chi^2_1 = 4.21$, $P = 0.04$; harmonics: $\chi^2_1 = 4.08$,

$P = 0.04$). Thus, it appears that the effect of intruder ID on the orienting responses of lone hyaenas can effectively be attributed to two acoustic properties of the whoop bouts: whoop duration and the RMS amplitude of the whoops.

Our use of calls recorded from outside of Kenya controlled for familiarity, but also introduced potential complications such as not knowing caller age or sex, and the use of calls from different locations. However, these variables did not appear to alter the responses of hyaenas to the playbacks. For example, country of origin had no apparent effect on orienting responses by lone hyaenas during the first whoop bout ($F_{2,20} = 1.65$, $P = 0.22$). Also, as noted above, we saw no indication that hyaenas responded differently to any calls based on minimum fundamental frequency.

Effect of Listener Group Size

Overall, four hyaenas, representing 33% of lone subjects, avoided the speaker, whereas no individuals in any group trial ever avoided the speaker. Across all three treatment conditions, final listener group size, defined as the number of clanmates present at the end of the trial, most strongly predicted whether hyaenas approached the speaker during a playback trial (Table 2). Specifically, lone individuals were significantly less likely to approach the speaker than were individuals in groups ($P = 0.004$; Table 2, Fig. 5a), and individuals in groups containing three or more hyaenas were significantly more likely to approach the speaker than were individuals in groups containing fewer than three individuals ($P = 0.006$; Table 2, Fig. 5a). Final group size predicted approach behaviour better than the presence of arriving individuals (AICc = 42.97 versus 45.93; Table 2), and the model with the lowest AICc value included only final group size as a predictor (Table 2). Neither rank of the focal hyaena nor the number of different intruder calls heard was a significant predictor of approach behaviour (Table 2).

Exact numerical odds did not significantly predict whether individuals would approach the speaker ($P = 0.12$; Table 2). However, individuals in groups with odds greater than 1:1 were significantly more likely to approach the speaker than individuals in groups with odds of less than or equal to 1:1 ($P = 0.013$; Table 2, Fig. 5b). With numerical odds greater than 1:1, hyaenas approached the speaker more than twice as often as hyaenas in groups with numerical odds

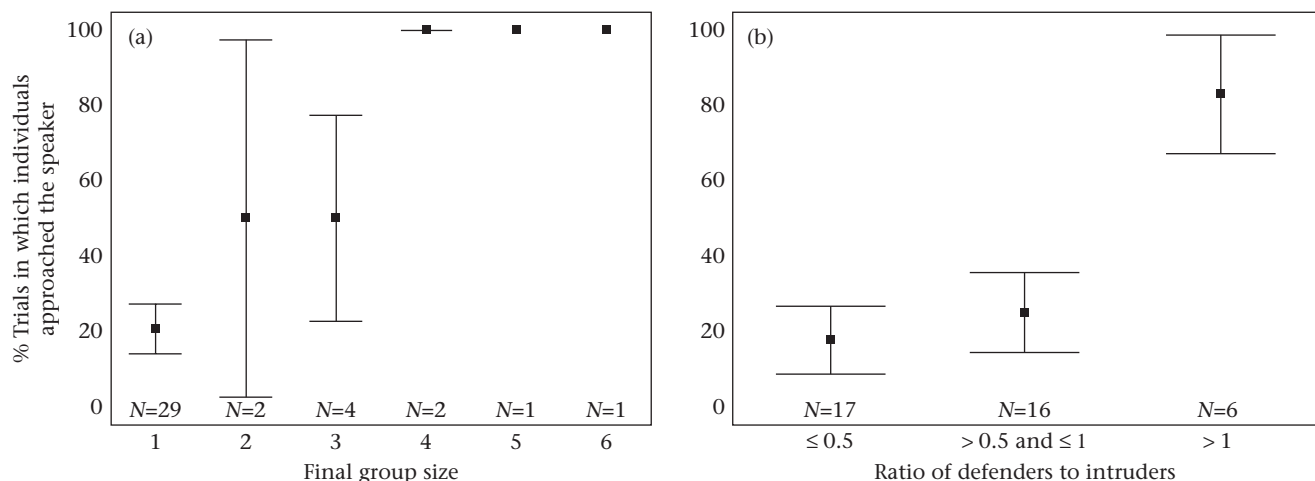


Figure 5. Mean \pm SE percentage of trials in which at least 50% of individuals approached the speaker as a function of (a) final group size and (b) numerical odds (ratio of final playback subjects ('defenders') to the number of different intruder calls played) in all playbacks conducted ($N = 39$). In (a), final group size included individuals that were not present at the start of the trial but that arrived during or immediately after the playback period. Focal hyaena(s) were considered to have approached the speaker if their position at the end of the trial was closer to the speaker than it was at sound onset, as assessed using a range finder. In (b), a ratio less than one represents a situation in which the number of intruders played was greater than the number of defenders present at the end of the trial. A ratio equal to one means that the number of intruders played equalled the number of defenders present. A ratio greater than one represents a situation in which defenders outnumbered intruders.

less than or equal to 1:1 (Fig. 5b). This appeared to be caused by a nonlinear effect of numerical odds on the probability of approaching the speaker. Indeed, there appeared to be a threshold effect of numerical odds such that hyaenas facing odds greater than one responded differently than hyaenas confronting odds less than one.

DISCUSSION

Our results support the following predictions of game theory: contest asymmetries can alter the cost/benefit ratio of entering into aggressive interactions, individuals should be more willing to engage in contests when they have the numerical advantage, and animals living in fission–fusion societies should be able to assess numerical odds. Specifically, we have shown that wild spotted hyaenas assess numerical advantage when exposed to calls from simulated intruders. The results support our prediction that wild hyaenas show more caution when they are outnumbered, indicated here by enhanced vigilance, and take more risks when the numerical odds are in their favour, indicated here by approaching the speaker. Spotted hyaenas thus show numerical assessment abilities comparable to those of lions, chimpanzees and howler monkeys (McComb et al. 1994; Wilson et al. 2001; Kitchen 2004). Furthermore, spotted hyaenas scale their vigilance based on the number of unique callers to which they are exposed, at least when there are three or fewer intruders calling. The results of this study thus provide the first experimental evidence that hyaenas use acoustic information available in whoops to differentiate among individual callers, supporting our prediction that hyaenas discriminate between individuals based on their calls.

Odds Ratios and Assessment of Numerical Advantage

Differences between trials involving lone hyaenas and those involving groups suggest that hyaenas have a fine-grained ability to assess numerical advantage. Lone hyaenas assessed risk, but they rarely approached the speaker, which fits with previous research showing that animals often require a substantial numerical advantage before engaging in an aggressive interaction, especially when potential rewards are not particularly large (Wilson et al. 2002). The risk of injury may not be worth the reward of chasing an intruding individual out of the territory, especially when the hyaena confronting intruders is not in the presence of a den, food, or vulnerable offspring. Although our sample size was small, we found that hyaenas in larger groups and with better numerical odds appeared to be more proactive, by approaching more often, when hearing the calls of intruding individuals.

Further work is necessary to investigate the cognitive mechanisms or representations used by hyaenas to assess numerical advantage. More research is also necessary to determine whether hyaenas respond based on small differences in numerical advantage even when confronted with larger numbers of intruders. We do not know whether there is a point at which this ability breaks down. It would be interesting to study the degree to which numerical advantage predicts outcomes of interclan territorial disputes.

We believe that hyaenas were responding to the number of unique callers because we controlled for other possible correlates of quantity, such as stimulus intensity and the number of whoops played. We reject the notion that hyaenas were simply showing a habituation/dishabituation response to the calls of intruders because hyaenas varied their approach behaviour based on numerical odds and their own group size, which we would not expect from a habituation/dishabituation response. The ability to assess numbers of unique callers may be particularly important for spotted hyaenas because hyaenas are often found in small subgroups in their

fission–fusion social system. In small subgroups, the presence of an additional group member or territorial intruder can significantly change the ratio of defenders to intruders, whereas in larger groups the presence or absence of a single individual will have less of an impact on numerical odds. Therefore, in small groups there is a substantial incentive to assess the precise number of individuals present before deciding to engage in an aggressive conflict.

Individual Differences in Vigilance

We expected hyaenas to follow predictions of game theory and respond differently to different numbers of intruders. Although a few females did react as expected and increase vigilance when there were more intruders, some females showed little variation in their responses to the three treatment conditions, which mostly involved a constant, high level of vigilance. Consistent differences in how individuals respond to the calls of territorial intruders has also been found in lions (Heinsohn & Packer 1995); some female lions consistently approached the speaker first, while other females consistently lagged behind their groupmates. Heinsohn & Packer (1995) could not attribute these differences in approach behaviour to any measure of fighting ability in lions, such as age or body size. We found no effect of rank on the responses of focal hyaenas to calls of conspecific intruders in the clan's territory, which matches a previous study showing that hyaenas of all social ranks participate in territorial advertisement and defence (Boydston et al. 2001).

Individual variation in vigilance responses might result from differences in what each individual has experienced in the recent past. Although possible, we think it is unlikely that one of our study animals heard an unknown intruder in the day preceding a playback experiment. We drive the home range of the focal hyaena(s) for several hours every morning and evening to record all sightings of unknown individuals within the home ranges of our study clans. We sighted unknown individuals on four separate occasions during the 11-month study period, and the shortest interval between sighting an unknown hyaena and conducting a playback experiment was 3 days. Given the low probability that our subjects had interacted with unknown hyaenas immediately before playbacks, the individual variation in vigilance responses observed here suggest personality differences, as does earlier work from our laboratory (Pangle & Holekamp 2010; Watts et al. 2010), but further research is needed to investigate this possibility.

Individual-based Vocal Discrimination

Hyaenas' responses to the playbacks seemed based on the numerical odds they faced, and not on the specific identity of the callers. However, we found evidence that hyaenas can distinguish among calls to assess numerical odds. Two vocalizations produced by spotted hyaenas, the whoop (East & Hofer 1991) and the giggle (Mathevon et al. 2010), have structural variation that might allow hyaenas to identify conspecifics as unique individuals. However, we cannot assume that animals can discriminate individuals by exploiting such individually variable acoustic signals (Schibler & Manser 2007). Individual variation in acoustic structure of vocalizations may have no adaptive function, and may simply be a by-product of morphological variation in callers. It is therefore important to test experimentally for individual discrimination in a wide variety of taxa, given how fundamental such discrimination abilities appear to be in the evolution of complex social cognition (de Waal & Tyack 2003).

Individual variation in the acoustic structure of vocalizations and the ability to discriminate individuals based on acoustic signals appear to be widespread among mammals (Cheney & Seyfarth 1988; Cheney et al. 1995; Blumstein & Daniel 2004; Wich & de Vries 2006). For example, male Thomas langur monkeys, *Presbytis*

thomasi, distinguish, keep track of, and remember group members (Wich & de Vries 2006), vervet monkeys, *Cercopithecus aethiops*, discriminate between individual callers (Cheney & Seyfarth 1988), and baboons, *Papio cynocephalus ursinus* (Cheney et al. 1995) recognize calls of specific female group members. Several studies have also used playback experiments to demonstrate recognition of groups of individuals, such as groupmates versus individuals from neighbouring groups or kin versus nonkin (McComb et al. 1993; Sayigh et al. 1999; Reby et al. 2001; Frommolt et al. 2003).

Prior to the current study, no experiments had been done asking whether hyaenas actually use the information in whoop or giggle vocalizations to distinguish among individuals. Our use of consecutive and nonoverlapping calls as sound stimuli required hyaenas to distinguish among individuals based on their vocalizations in order to determine the number of unique callers. In addition, because the stimulus calls were not played simultaneously, focal hyaenas had to remember which calls they had heard earlier to identify novel calls. Had hyaenas simply been counting calls without distinguishing among them, the responses observed in all three playback treatments should have been statistically indistinguishable, but that was not the case.

This result is consistent with previous findings on the cognitive abilities of spotted hyaenas. For example, previous playback experiments indicated that hyaenas recognize certain classes of individuals, such as maternal kin and offspring, from their whoop vocalizations (Holekamp et al. 1999). In addition, hyaenas demonstrate complex social cognitive abilities that appear to require individual recognition, including recognition of third-party relationships among group members (Engh et al. 2005), and individual assessment of potential social partners based on their relative value (Smith et al. 2007). Interestingly, spotted hyaenas also show individual discrimination in chemical signals; Drea et al. (2002) performed a habituation–dishabituation experiment to show that males discriminate between novel and familiar scents of females in a single reproductive state. Thus, hyaenas can discriminate individuals using multiple sensory modalities.

Conclusion

Spotted hyaenas conform to predictions of game theory and show comparable abilities to assess numerical advantage to those seen in lions, chimpanzees and howler monkeys. Hyaenas also assess the number of unique callers, thereby demonstrating an ability to discriminate among individuals based on their vocalizations. Spotted hyaenas live in complex societies, and social complexity is thought to be a major driving force in the evolution of complex cognitive abilities in mammals. Our findings support this idea by providing evidence that primates and carnivores with similarly complex social systems have evolved similarly complex abilities to assess numerical advantage.

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