



RESEARCH PAPER

African Wild Dogs as a Fugitive Species: Playback Experiments Investigate How Wild Dogs Respond to their Major Competitors

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Abstract

It has been suggested that African wild dogs *Lycaon pictus* need exceptionally large home ranges (and hence occur at such low densities) because they are limited by competition with larger sympatric carnivores, namely lions *Panthera leo* and spotted hyenas *Crocuta crocuta*. To investigate this relationship at a proximate level and explore which factors mediate it, we conducted audio playback experiments examining how wild dogs responded to the simulated proximity of either lions or hyenas. The principle finding was that wild dogs consistently moved directly away from lion roars, but when played hyena whoops either stood their ground or, later, moved off in a random direction. These results suggest that lions represent an immediate high-level threat to wild dogs that is invariably best avoided, whilst the threat from hyenas may not be so great or perhaps is simply unavoidable. Wild dogs appeared to make some assessment of ambush risk during interactions with lions, illustrated by the varying latency to their retreat in habitats of differing vegetation density (and hence ambush potential). Additionally, packs with younger pups were more likely to alarm call and exhibited a slower rate of retreat in the hour following exposure to lion roars. Other variables investigated (competitor group size, lion sex, presence of pups) failed to explain variation in wild dogs' responses.

Introduction

Interference (direct) and exploitative (indirect) inter-specific competition are of potential importance for a large number of carnivore species and may limit the numbers or distribution of weaker competitors (Palomares & Caro 1999; Linnell & Strand 2000; Caro & Stoner 2003; Donadio & Buskirk 2006). Models show that the persistence of weaker species alongside superior competitors depends on either temporal fluctuations in the environment (Chesson & Warner 1981) or, more often, the existence of spatial heterogeneity (Chesson 1985; Hanski 1994). Such fugitive species can therefore best avoid dangerous competitors by finding empty habitat patches or simply utilizing a different kind of patch (Shorrocks 1991).

Creel & Creel (2002) suggest African wild dogs occupy extensive home ranges to provide themselves with some potential degree of spatiotemporal isolation from dominant sympatric competitors, specifically lions and spotted hyenas. Additionally, Saleni et al. (2007) report that wild dogs exhibit sequentially dissimilar temporal activity patterns to those of lions and hyenas. Greater spatial coexistence may be possible in areas with lower prey densities, where lions and hyenas are scarcer (Holt & Polis 1997). However, the threat from larger competitors means fugitive wild dogs are often excluded from (or may only temporarily visit) areas supporting the highest prey and predator densities (Mills & Gorman 1997).

Lions directly limit wild dogs by stealing their kills, killing pups or even adults. Indeed, lions may be the

single greatest cause of natural mortality for wild dogs, with lion predation accounting for 47% of known-cause adult wild dog deaths in the Moremi Game Reserve (J. W. McNutt, pers. comm.).

By contrast, Woodroffe & Ginsberg (1999) estimate that hyena predation across several populations (primarily in the Kruger National Park, Hwange National Park and Selous Game Reserve) accounts for just 4% of adult wild dog mortality and 6% of pup mortality. Whilst hyenas probably kill wild dogs less often than lions do, they nevertheless often kleptoparasitize wild dog kills. Because wild dogs operate on tight energy budgets (Gorman et al. 1998; Rasmussen et al. 2008), regularly losing kills could still have strong and directly limiting effects on wild dogs.

The sum of all this competitive inhibition is thought to explain the inverse correlation observed between the densities of wild dogs and those of their two larger competitors (Creel & Creel 1996, 2002). The scarcity of wild dogs in areas dominated by lions and hyenas may derive from active avoidance (potentially reducing foraging success, see Durant 2000a) and/or demographic effects (increased mortality from intraguild predation). However, because Creel & Creel (2002) also report a strong positive correlation between lion and hyena densities, it is not immediately clear whether both lions and hyenas restrict wild dog density to an equal extent.

Creel et al. (2001) report that wild dogs moved away from 11 of 12 trial audiotape playbacks of lion roars, but similar trials using hyena whoops were not part of their study. To fully investigate the respective roles of lions vs. hyenas in competitively inhibiting wild dogs (and examine which factors might mediate these interactions), we conducted playbacks to directly monitor and compare wild dogs' responses to the simulated presence of nearby lions and hyenas. We predicted (1) that predatory lions should be more actively avoided than hyenas; and (2) that wild dogs' responses may be mediated by factors influencing the likely outcome of overt conflict.

To test these two predictions we examined (1) whether wild dogs responded differently to lions vs. hyenas and; (2) whether responses were affected by caller group composition, e.g. the sex of the roaring lions (male lions, being larger, might constitute a greater threat), or indeed by the size of the calling group (singletons might constitute a lesser or more manageable threat than groups of three lions or hyenas). We also investigated whether factors such as habitat density (associated with ambush risk), the presence and age of potentially vulnerable pups within wild dog groups, or the size (and hence

strength) of the wild dog pack subjected to these playbacks, influenced the dogs' responses.

Methods

Study site

The study area was composed of a mosaic of seasonally flooded grasslands, mopane woodland and acacia savannah covering approx. 2600 km² centred around S19.5 E23.5 (decimal degrees WGS 84) in the eastern Okavango Delta in northern Botswana (see McNutt 1995 for details).

Playback protocol

We used audio playback experiments as a means to explore and quantify rarely observed interspecific interactions. From June 2005 to November 2007, we conducted 31 playbacks of lion roars and hyena whoops to eight packs of free-ranging wild dogs, these being diagnostic call types used by lions and hyenas for long distance communication (East & Hofer 1991; Pfefferle et al. 2007). Drs Karen McComb and Jon Grinnell made the recordings of lion roars in the Serengeti National Park between 1988 and 1991 using a Panasonic SV250 digital audio tape recorder (frequency response 10Hz–22 kHz; Panasonic, Secaucus, NJ, USA) and Sennheiser MKH 816 microphone (frequency response 40 Hz–20 kHz; Sennheiser Electronic GmbH & Co., Wedemark, Germany).

Playback stimuli from these recordings, of both male and female lions, consisted of individuals presented as singletons, i.e. roaring alone, and also presented in a paired stimulus recording with the same lion now roaring as part of a chorus of three (i.e. with two other lions). These choruses included both naturally occurring exemplars and exemplars constructed by sound mixing (McComb 1992). Their use allowed us to examine any effects owing to differences in the number of callers (1 vs. 3) whilst controlling for caller identity (see McComb et al. 1994). Lion exemplars (Table 1) were coded with a group of letters/numbers (e.g. SMC and MS10) labelling the callers in the sequence.

Recordings of hyenas were obtained from Dr Sarah Durant, who also made her recordings in the Serengeti using a Sennheiser MKH 816 microphone linked to a Sony TCD3 or Sony TCD7 digital audio tape recorder (frequency response for both 20 Hz–22 kHz; Sony Manufacturing Systems Europe, Weybridge, UK). Information on the sex of these hyenas was unavailable, but it was possible to con-

Table 1: Summary of playbacks (exemplar^a was played first of pair)

Pack Yr	1 lion exemplar		3 lions chorus exemplar		1 hyena exemplar	3 hyenas chorus exemplar
	Male	Female	Males	Females		
Matthews 05		SMC		3SMC ^a	S ^a	3 S
Matthews 06	SNAG		3SNAG ^a			
Mathews 07	MS10 ^a		3MS10		W	3 W ^a
Xakanaxa 05-06		LO5		3 LO5 ^a	W ^a	3 W
Xakanaxa 07	SNAG ^a		3SNAG			
Chitabe 05-06		LO5		3 LO5 ^a	S ^a	3 S
Mankwe 06					K	3 K ^a
Mankwe 07		SMC ^a		3 SMC		
Agate 05				3 SMC	S	
Motopi 05			3 LO5			
Labrador 07					K	3 K ^a
Himba 07					S	3 S ^a

struct choruses of three hyenas containing a known individual singleton calling with 2 others using sound mixing techniques (McComb 1992). Accordingly, we constructed three matched pairs of 3 vs. 1 hyena callers (see Table 1). All these recordings (lion and hyena) were originally made with digital audio-tape but were transformed to .wav files for this study. The order of presentation to the wild dogs of the matched pairs of recordings (singleton vs. chorus) was randomised to control for habituation effects.

We played back our recordings through a Tannoy CPA 12 studio monitor loudspeaker (frequency response 50 Hz–25 kHz \pm 3 dB; Tannoy Ltd., Coatbridge, UK) powered by a Kicker Impulse car amplifier (frequency response 20 Hz – 20 kHz \pm 0.5 dB; Stillwater Designs, Stillwater, OK, USA) linked to a Fostex FR2 recorder (frequency response 20 Hz–40 kHz \pm 2 dB; Fostex, Tokyo, Japan) operated from within a 4 wheel drive vehicle. Lion and hyena calls were all standardised to 110 dB re 20 μ Pa (peak intensity checked at 1 m using handheld AZ Analog Sound Level Meter model 8926; Laesent International Co. Ltd, Shenzhen, China) – well within the range of variation of natural sound pressure levels observed for these species (see Durant 2000b).

Experiments were conducted up to an hour and a half after sunrise or with less than an hour and a half before sunset – periods when principally nocturnal carnivores might yet naturally hear each other, but when there was sufficient light to make observations. We placed the loudspeaker 100 m from each subject pack, checking the distance with a pair of Buckmaster Rangefinders (accurate to \pm 1 m from 10 to 400 m, Nikon Corporation, Tokyo, Japan) making consistent efforts to place the loudspeaker out of sight behind available vegetation. The loudspeaker

was connected to the observation vehicle by 100 m of speaker cable; this vehicle was parked to one side so as to observe the subject pack, the loudspeaker and the area in between.

Lion roar exemplars had a duration of 29–67 s (\bar{x} = 43.6, SD = 12.4) and hyena whoop exemplars a duration of 33–50 s (\bar{x} = 39.3, SD = 6.4). Lion roaring bouts typically include more discrete calls within a calling bout than do hyenas, partly because roaring bouts end with repetitive lower-amplitude grunts. To account for these factors, we included playback duration and number of calls as covariates in our analyses.

We played all recordings twice. The second playback was started after a silent interlude, 2 min after commencing the first. Each pack's response to these playbacks was videotaped using a Canon Digital Video Camcorder (model MV800; Canon Inc., Tokyo, Japan). Playbacks were initiated once we had recorded at least two continuous minutes of video of the pack at rest, during which time all adult dogs were observed to be dozing, thus ensuring that the dogs were relaxed and settled ahead of the experiment (we simply re-started the video recording should any adult dog move during this period). We continued video recording after the playbacks until the last dog moved off or, when the playbacks failed to provoke a pack movement, for 5 min.

When playbacks provoked a pack to move off, we noted the direction of movement (in relation to the loudspeaker) and later analysed the video recording to calculate each fleeing pack's latency to retreat (scored as the time elapsed from the moment the first dog responded by raising its head following playbacks, to the time of the last dog's final departure on the pack's retreat) and whether any pack member was

stimulated by the playbacks to give a recognisable alarm vocalisation (a bark or a growl). Packs were monitored for 1 h after playback, so that should they become active after the initial response and video recording had ceased, we still had a record of the time of their subsequent departure (e.g. moving off on evening hunt). Having taken a GPS fix (eTrex, accurate to ± 10 m; Garmin International, Inc. Kansas City, MO, USA) of each pack's resting location at the playback's start, the pack's position was again noted 1 h later.

Other factors that could influence the behaviour of wild dogs such as pack size (number of dogs >1 yr old), whether packs contained pups (known individuals <1 yr old – individuals, including pups, could be reliably identified by their unique coat patterns (Maddock & Mills 1994)), pup age (calculated in wk from known parturition date) and habitat density (scored for the vicinity of each playback on a scale of 1–3, with 1 meaning mostly open, e.g. flood plains, 2 being areas of intermediate vegetation density, i.e. anywhere that offered some cover but was not exceptionally thickly vegetated, and 3 being markedly dense areas with limited visibility, e.g. riverine vegetation or thick scrub) were also recorded.

At least 2 wk were allowed to elapse between playbacks of any sort to the same pack so as to prevent habituation. The same exemplars were sometimes tested on different packs, but the same pack was never exposed to the same exemplar twice (see Table 1). When the same wild dog pack was presented with more than one pair of playbacks of the same stimulus type (lion or hyena), long intervals (average 6 mo) were left between successive playbacks and different exemplars of that stimulus type were utilised. Where repetition of stimulus type was unavoidable, this approach (using different exemplars and maintaining very significant temporal interludes) was the only practical solution to the problem of sample size, given the rarity and extreme low density of the study species (Wiley 2003). Additionally, we were careful to use statistical models that accounted for pack identity as a random factor.

Analyses

A series of linear mixed models (with a scaled identity covariance structure, using a maximum likelihood estimation) were constructed in SPSS (SPSS Inc., Chicago, IL, USA) to individually examine in turn the effect of different independent, fixed variables (predator stimulus type, habitat density, number of callers, lion sex, pack size, presence of pups

and pup age) on the four dependent variables (whether dogs approached the loudspeaker or called in alarm, their latency to retreat and the distance moved in the hour following playbacks). Within these models, pack identity was set as a random effect to account for repeated sampling whilst playback duration and number of calls were included as covariates. Owing to our relatively small sample size, it was not possible to build a model that included all the independent variables simultaneously because of the effects of over-parameterisation and subsequent need to limit the number of fixed effects in each model.

However, to examine in greater detail the effect of different variables on the dogs' responses exclusively following playback of lion roars, various models were constructed and compared (see Tables S1 to S4), keeping pack identity as a random effect, but with different combinations of fixed factors; playback duration and number of calls were kept as covariates. The fit of potential models was determined using Akaike's Information Criterion corrected for small samples (AICc) and ranked using AICc to determine the best fit model (Burnham & Anderson 2002).

Neither pack exemplar nor exemplar presentation order had any effect on the dogs' responses and so separate playbacks to the same pack could be considered independent (McGregor et al. 1992). Thus, although we identified the number of packs as a limiting factor, their repeated use proved justified.

Results

Which species do wild dogs avoid?

Wild dogs responded very strongly to playbacks of lion roars. Their response typically started with them rising to a standing position with the head facing and ears pricked towards the loudspeaker. Following this, one or more dogs frequently (64% of all lion playbacks) approached a short distance (2–60 m) towards the loudspeaker (although no approaches were recorded in the densest habitat). In intermediate-density habitats, dogs were sometimes additionally observed rearing on their hind legs (after 33% of playbacks in such habitats) whilst looking towards the sound's source (Fig. 1 and Video clip S1 in supporting information). Both the partial approach and the rearing behaviour appeared to be attempts to get a visual fix on the simulated lion(s). In dense habitats, dogs neither approached nor reared up, but instead only retreated in apparent haste (see Fig. 2).

Invariably, within 15 min of the first playback of lion roars, packs began a steady trot away from the

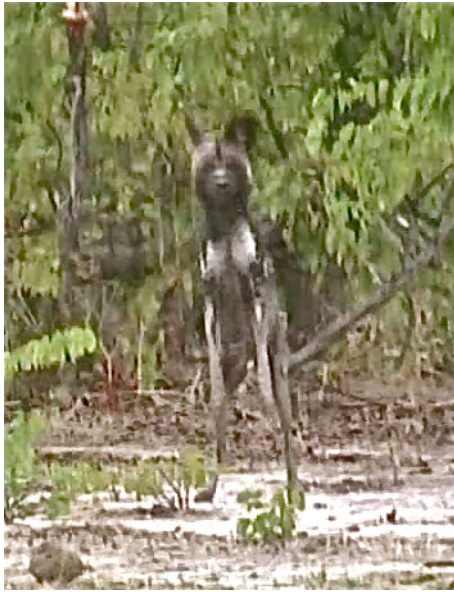


Fig. 1: Wild dog in alarmed rearing posture (video clip included in electronic supplementary material).

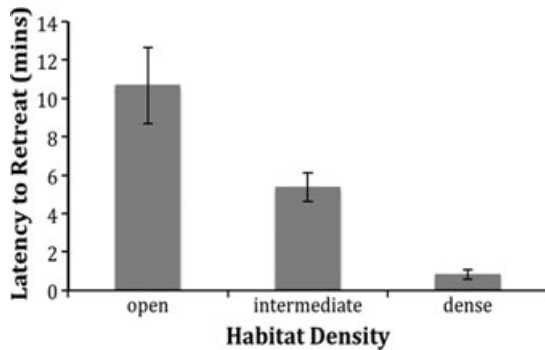


Fig. 2: Bar chart illustrating ± 1 SE of the mean latency to wild dog packs' retreats from lion roars in habitats of differing density (Open $N = 3$, Intermediate $N = 9$, Dense $N = 2$).

location of the loudspeaker; an hour later, they were on average 1.9 km (range 0.6–3.2 km) away from the experiment's starting point. In the time that elapsed between playbacks and the departure of the last dog, every pack maintained sustained vigilant behaviour directed towards the loudspeaker. The vocal greetings customary ahead of pack movements were truncated or omitted entirely (57% of retreats occurred without them).

By contrast, wild dogs never retreated directly away from the loudspeaker following playbacks of hyena whoops, as they ultimately did after hearing lion roars (See Fig. 3). Instead, they commonly (after 47% of hyena playbacks) returned to a state of non-

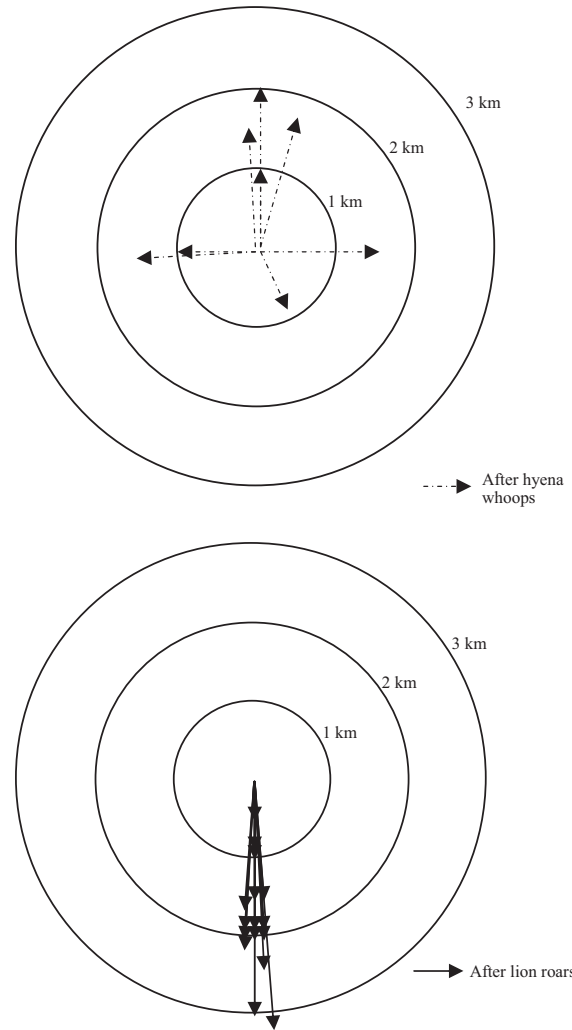


Fig. 3: Wagon wheel illustrating direction and distance travelled when packs moved off in the hour following playbacks; the wheel is orientated so that the subject pack starts at the wheel's centre and the loudspeaker is 100 m north of this centre point.

vigilant repose (all adult pack members dozing) within 5 min of the initial hyena playback, remaining unmoved in the subsequent hour's observation and showing an apparent lack of concern for the perceived proximity of hyenas.

On other occasions (after 47% of hyena playbacks), one or more dogs partially or fully approached (up to or beyond) the loudspeaker. Overall, whilst wild dogs sometimes approached the loudspeaker (at least partially) following playbacks of both lion roars and hyena whoops, they were no more or less likely to do so for either particular stimulus type ($F_{1,28} = 0.403$, $p = 0.531$). However, it was noted that completed approaches (moving right up

to or past the loudspeaker) only occurred following hyena playbacks, and approaches following hyena whoops were all conducted without the accompanying alarm calls or rearing that typified a partial approach in response to lion roars.

Owing to all experiments being conducted within the dogs' crepuscular activity period, packs did occasionally (after 53% of hyena playbacks) spontaneously become active and begin to move off on hunts within the hour they were monitored following each experiment. However, wild dogs were significantly more likely to move off in the first 10 min following playback of lion roars than they were after hearing hyena whoops (Table 2; $F_{1,30} = 11.471$, $p = 0.002$). Furthermore, whilst the dogs always moved directly away from playbacks of lion roars, their direction of movement in the hour following playbacks of hyena whoops was apparently random (see Fig. 3). These movements also found them on average only 0.7 km (range 0.0–2.0 km) away from the experiment's starting point after 1 h, i.e. significantly less far than they were following lion roars ($F_{1,30} = 12.521$, $p = 0.001$).

Playbacks of lion roars also often prompted alarm calling amongst the dogs (after 64% of lion playbacks); occasionally, these calls took the form of loud, modulated barks (signalling extreme alarm), but often vocalisations were limited to low-amplitude warning growls. Overall, lion roars were much more likely to elicit alarm calls than hyena whoops (Table 2; $F_{1,28} = 10.945$, $p = 0.003$).

Table 2: Wild dog responses to lion roars ($N = 16$) vs. hyena whoops ($N = 15$). On two occasions, the wild dogs' vocal and approach responses to playbacks of three lions could not be clearly observed/determined (F = female lions, M = male lions). Packs were noted to have moved off if they departed within 10 min following the start of playbacks. Approaches were recorded if any individual within the pack made any movement of more than 5 m towards the loudspeaker following playbacks

Playback type	No		Approach	Pack		
	Alarm call	alarm call		No approach	moves off	Pack stays
1 lion roars	4	3	4	3	5	2
(F)	(2)	(2)	(3)	(1)	(3)	(1)
(M)	(2)	(1)	(1)	(2)	(2)	(1)
3 lions roar	5	2	5	2	8	1
(F)	(3)	(1)	(3)	(1)	(6)	(0)
(M)	(2)	(1)	(2)	(1)	(2)	(1)
Total lions	9	5	9	5	13	3
1 hyena	0	8	3	5	1	7
3 hyenas	0	7	4	3	1	6
Total hyenas	0	15	7	8	2	13

Numerical assessment

The number of callers in each playback had no significant effect on any of the recorded responses from subject packs. There was no difference in the likelihood of an approach based on the number of predators calling ($F_{1,28} = 1.944$, $p = 0.174$), nor did the number of predators in each playback explain the variation in distance moved in the following hour in response to the two stimulus types ($F_{1,30} = 0.074$, $p = 0.788$) or the latency to departure ($F_{1,28} = 0.008$, $p = 0.931$).

Lion roars elicited stronger responses from the dogs, but the number of lions roaring appeared to have no effect on the latency to pack departure ($F_{1,13} = 0.339$, $p = 0.570$) or the distance subsequently moved in the following hour ($F_{1,15} = 1.602$, $p = 0.225$). Furthermore, although wild dogs only ever barked or growled in response to lion playbacks, the number of lions roaring in these playbacks had no effect on the likelihood of the dogs giving these alarm calls ($F_{1,13} = 2.159$, $p = 0.164$).

Other factors

The *only* variable consistently explaining the dogs' responses to both lion roars and hyenas whoops was predator type (latency to retreat: $F_{1,28} = 17.967$, $p < 0.001$; distance moved: $F_{1,30} = 12.521$, $p = 0.001$), such that dogs retreated quicker and moved further away from lion roars. Other variables (habitat, competitor group size, pup presence, pup age or pack size) were all non-significant when considering the dogs' responses to lion roars and hyena whoops together.

Considering then only those experiments involving playback of lion roars, habitat density alone was the best predictor of the latency to the last dog's retreat ($F_{1,13} = 23.189$, $p < 0.001$); wild dogs were significantly slower to move away from lion roars when in open habitats, which afforded clear lines of sight in the direction from which the roars and hence threat came (Fig. 2). Habitat density was also the best predictor of whether packs approached the loudspeaker ($F_{1,13} = 4.476$, $p = 0.031$), with packs least likely to venture any approach in the densest habitats.

Pup age proved to be the best predictor of whether packs alarm called and the distance packs moved following exposure to lion roars; specifically, packs with younger pups were more likely to alarm call ($F_{1,13} = 21.385$, $p < 0.001$) and moved less far in the hour following playback ($F_{1,15} = 9.208$, $p = 0.001$).

None of the other independent variables examined contributed to the best fit models selected by their AICc scores (see Supporting Information).

Discussion

Where previous studies have simply shown an inverse density relationship between lions and hyenas on the one hand and wild dogs on the other, our results provide more specific insight by showing that lions, far more than hyenas, are the species that wild dogs actively seek to avoid.

Experiment-based investigation into a species as rare and wide ranging as the African wild dog (Ginsberg & Woodroffe 1997) encounters problems related to small sample size and animal and stimulus re-use, constraining the potential for statistical analysis. Our only practically available solution to this was to control for pack identity within our analyses and leave significant temporal gaps between playbacks (Wiley 2003). However, even given the constraints of sample size, a number of strongly significant results emerged from our experiments.

Foremost amongst these was the avoidance behaviour exhibited by wild dogs when confronted with lion roars. This behaviour is costly in terms of time, energy expended or having to move away from the best hunting areas (Durant 2000a). Wild dogs' greater reluctance to move away from hyena whoops suggests the *immediate* direct threat hyenas present may be lower than that presented by lions, such that it is outweighed by these avoidance costs. This 'lower-threat hypothesis' is supported by observations of hyenas only rarely approaching playback of wild dog vocalisations, unlike lions, which consistently approached the same calls (Webster et al. 2010).

Alternatively, rather than hyenas representing a lower threat than lions, the different responses observed amongst the dogs might be best explained in terms of behavioural switches to different types of threats (e.g. Lima & Bednekoff 1999). Lions may be easily outrun, so avoidance behaviour constitutes a good solution to detection of nearby lions. By contrast, because hyenas are more numerous, more evenly dispersed across the landscape, have greater stamina and may be more persistent in following wild dogs, avoidance of this species may be impossible (Creel et al. 2001). Hence, standing ground or chasing them off is a better strategy.

However, different *types* of threat in this instance also likely correspond with different *levels* of threat, as indicated by our finding that the dogs were more

likely to alarm call in response to playbacks of lion roars. Furthermore, wild dogs only completed approaches (moving right up to or past the loudspeaker) following exposure to hyena whoops. This could indicate a greater willingness to engage closely in a potential mobbing response to hyenas, contrasting with partial approaches limited to visually verifying the location of an audible threat (e.g. the rearing behaviour observed during partial approaches towards lion roars).

The limited response of wild dogs to playbacks of hyena whoops in our study suggests that the direct competition that does exist between hyenas and wild dogs may not invariably have the impact previously documented in the Serengeti (Carbone et al. 2005). Furthermore, a careful reading of accounts typically referenced in support of the argument that scavenging hyenas have a significant detrimental impact on wild dogs reveals that hyenas frequently only successfully kleptoparasitize kills *after* wild dogs have eaten extensively (e.g. Fanshawe et al. 1991; Fanshawe & Fitzgibbon 1993); indeed, wild dogs are quite capable of mobbing individual hyenas in defence of a kill or pups (H. Webster pers. obs.).

We cannot rule out the other possibility that hyenas, because they share considerable dietary overlap with wild dogs (Hayward & Kerley 2008; Owen-Smith & Mills 2008), might still limit wild dogs to some extent by indirect competition. However, this remains unlikely because wild dogs are extremely efficient hunters able to successfully exploit even very low prey densities (Ginsberg & Woodroffe 1997).

Wild dogs were more likely to stand their ground or partially approach in response to lion roars when in open environments, than when in dense habitats, where the risk of ambush is greater. A similar response is reported amongst shorebirds (Metcalf 1984) and African antelope (Underwood 1982). Grinnell et al. (1995) also report that lions spread out more in thicker cover when approaching a loudspeaker after playback of intruder males. By hastening their retreat in dense habitats, wild dogs appear to perform at least a functional level of risk assessment in response to the greater threat of an ambush attack in thick cover.

This finding does not however mean that wild dogs will fare better in competition with lions in entirely open habitats because lions (and hyenas) locate wild dogs and their kills most easily in open habitats (Creel 2001). Thus, although wild dogs may better avoid ambush in open habitats, the regularity of kleptoparasitism events in open areas makes them sub-optimal

(Gorman et al. 1998). Wild dogs may instead ideally occupy extensively canopied woodland with a minimal understory (e.g. mature mopane) that supports low-to-intermediate prey densities, in turn supporting lower competitor densities. Such a habitat would make it less likely that vultures or competitors locate wild dog kills but might also provide occasional clearings in which wild dogs can rest up without risk of ambush.

The undifferentiated responses amongst packs exposed to 1 vs. 3 lions may be explained in several ways. One possibility is that although all lions within a group do typically roar together and lions themselves gauge group size from the number of roars (McComb et al. 1994), wild dogs may instead assess the roar of one lion to mean that there may be several nearby. Alternatively, it is probable that one lion is simply sufficiently dangerous to provoke a maximal alarm response.

Conversely, hyenas apparently present so little threat to resting wild dogs that they exhibited a consistent *lack* of response to both one and three callers. However, at kill sites, hyenas may still present a significant threat if they are able to steal the wild dogs' food. In such instances, wild dog pack size may principally affect their ability to repel attempted kleptoparasitism by hyenas (Gorman et al. 1998).

Interestingly, packs with younger pups were more likely to alarm call following exposure to lion roars, and this suggests an increased sensitivity to risk when accompanied by younger pups. Young meerkats have been found to need experience during early development to associate an alarm call correctly with the type of threat and appropriate response (Hollén & Manser 2006). Wild dog reintroduction attempts now commonly involve captive bred dogs that have been bonded with wild caught adults in a boma prior to their release, partly because captive bred dogs may otherwise underestimate the risk posed by lions (Gusset et al. 2006).

The finding that packs with younger pups moved less far in the hour following exposure to lion roars suggests that whilst accompanied by young pups, packs are limited in the rate of their movements. If this is the case, it may extend the period dogs must remain active to cover the same ground, be it hunting or patrolling their territory, with potential ramifications for prey or competitor encounter rates (Saleni et al. 2007).

In conclusion, our results indicate that wild dogs actively avoid lions in all situations, suggesting that lions may limit wild dogs' access to areas where they encounter lions too frequently. This provides further

evidence that wild dog reintroduction attempts should avoid areas inhabited by dense populations of lions (Creel 2001; Creel et al. 2001) and be focused on areas large enough to provide spatial refuges for this fugitive species (Durant 1998). In contrast, wild dogs did not actively avoid hyenas in our study, which may either suggest they are perceived as a lesser threat or that efforts to avoid them may not be energetically worthwhile. It remains possible that too frequent kleptoparasitism by hyenas locating wild dog kills in very open habitats may have a significant detrimental impact on wild dog energy budgets and hence pack success (Gorman et al. 1998). However, our results indicate that when faced with a potential direct encounter with lions or hyenas, it is lions that wild dogs actively seek to avoid.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1: Top four *a priori* hypothesized models explaining the wild dogs' latency to retreat from playback of lion roars.

Table S2: Top four *a priori* hypothesized models explaining the wild dogs' likelihood of alarm calling following playback of lion roars.

Table S3: Top four *a priori* hypothesized models explaining the wild dogs' likelihood of approaching the loudspeaker following playback of lion roars.

Table S4: Top four *a priori* hypothesized models explaining the distance moved by wild dogs following playback of lion roars.

Video Clip S1: Wild dog alarm barks and rearing up on hind legs in response to playback of lion roars.

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