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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.

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