Animal Behaviour 105 (2015) 187–200

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Collective movements, leadership and consensus costs at reunions in spotted hyaenas

Jennifer E. Smith [a,*], Jillian R. Estrada [b], Heather R. Richards [b], Stephanie E. Dawes [b], Kari Mitsos [b], Kay E. Holekamp [b]

[a] Biology Department, Mills College, Oakland, CA, U.S.A.
[b] Department of Integrative Biology, Michigan State University, East Lansing, MI, U.S.A.

ARTICLE INFO

Article history:
Received 19 September 2014
Initial acceptance 10 October 2014
Final acceptance 23 March 2015
Published online
MS. number: A14-00753R2

Keywords:
consensus cost
Crocuta crocuta
fission–fusion
group living
group travel
leader–follower
reunion
spotted hyaena

Because collective movements have fitness consequences for all participants, group travel can impose conflicts of interest when group-mates vary. Challenges associated with coordinating activities of group-mates, such as during travel, may potentially be mitigated through the use of simple rules governing leadership and other behaviours to minimize conflict. Although individuals living in groups with fission–fusion dynamics may temporarily separate, leadership determination at subsequent reunions, and events occurring during reunions, are poorly understood. Here we investigate leadership during travel prior to reunions of spotted hyaenas, *Crocuta crocuta*, living in one large social group in the Masai Mara National Reserve, Kenya. Whereas individuals often arrived at dens or joined hunting parties alone, those joining others to participate in group defence of shared resources typically did so when accompanied by group-mates. Although most hyaenas led processions, the attributes of members within each travelling party consistently predicted leadership roles. The highest-ranking adult within each travelling subgroup, often a lactating female, typically assumed the vanguard position prior to reunions. Reunions promoted conflict, particularly at kills. However, as predicted by the conflict mitigation hypothesis, individuals that greeted conspecifics were significantly less likely to fight at reunions than were hyaenas that failed to greet at reunions. Thus, whereas temporary separations may reduce immediate conflicts of interest in fission–fusion societies, hyaenas pay consensus costs at subsequent reunions, particularly in the context of feeding competition, and greetings appear to reduce such costs. Finally, we propose a novel scheme for leadership categorization in which leadership depends on whether or not leadership is based on specific attributes of individual group members. We apply this attribute-based framework to quantify the patterns and mechanisms of leadership during group travel for 52 species of mammals, including the spotted hyaenas studied here, and place findings in a broad evolutionary context.

Collective movement occurs when two or more individuals maintain spatial proximity while travelling together to a new location (Petit & Bon, 2010). This phenomenon occurs in insect swarms, schools of fish, bird flocks, herds of mammalian herbivores, cetacean pods, carnivore groups, troops of nonhuman primates and human crowds (reviewed by Conradt & Roper, 2009). Group travel that requires all group-mates to choose between collectively moving to a new location and remaining together in their current location represents a 'consensus decision' (Conradt & Roper, 2003). Because travel decisions often have fitness consequences for all participants (e.g. Dostálková & Spinka, 2007; Rands, Cowlishaw, Pettifor, Rowcliffe, & Johnstone, 2003), consensus decisions can impose conflicts of interest among group members when individuals vary in the extent to which they benefit from mutually exclusive travel options (Conradt & Roper, 2005). For example, consensus decisions may require all members to settle on a single direction, timing or destination of group travel. Potential conflicts of interest represent 'concensus costs'.

In social species, individuals must regularly negotiate conflicting interests among group-mates that vary in their optimality criteria (Alexander, 1974). Various challenges associated with coordinating the activities of group-mates, such as during travel, may therefore be potentially mitigated through the use of simple rules governing leadership and other behaviours that minimize consensus costs. Leadership during group travel may occur with or without a

* Correspondence: J. E. Smith, Biology Department, Mills College, 5000 MacArthur Blvd, Oakland, CA 94613, U.S.A.
E-mail address: jesmith@mills.edu (J. E. Smith).

http://dx.doi.org/10.1016/j.anbehav.2015.04.023

centralized organizer or a shared understanding of the roles of individual participants during group travel (Couzin & Krause, 2003; Couzin, Krause, Franks, & Levin, 2005; Petit & Bon, 2010). During group travel, 'leaders' may emerge when one individual, the 'leader', is followed by one or more conspecifics ('followers') as he/she moves towards a new location or initiates an action requiring coordination (King, 2010; Krause, Hoares, Krause, Hemelrijk, & Rubenstein, 2000). Although there is a growing understanding of the factors influencing leadership decisions (e.g. Boinski & Garber, 2000), a new synthesis of this body of work is needed to understand the general patterns and mechanisms of leadership during group travel among mammals.

Species living in groups structured by fission–fusion dynamics mitigate many of the costs associated with group living (e.g. feeding competition, fighting) without sacrificing benefits accruing from collective action (Aureli et al., 2008; Kerth, 2010; Smith, Kolowski, Graham, Dawes, & Holekamp, 2008). Individual members of fission–fusion societies avoid potential conflicts of interest (consensus costs) by splitting apart from and later rejoining other members of their social group (Conradt & Roper, 2000, 2005). Subgroup fissions occur when one or more individuals temporarily separate from others, and subgroup fusions (hereafter referred to as 'reunions') occur when individuals come back together. However, we currently know very little about subgroup travel decisions prior to reunions within fission–fusion societies. Importantly, we also lack an understanding of the social and ecological circumstances determining leadership at reunions, and whether leaders possess particular attributes or behaviours that promote followership. The functional consequences of subgroup reunions are also unclear.

We attempt to fill these gaps by quantifying the patterns and mechanisms of group travel among mammals in general and by elucidating the principles governing leadership at reunions in a gregarious carnivore, the spotted hyaena, *Crocuta crocuta*. Here a leader was identified as such only when an individual member of a travelling subgroup actively promoted social cohesion between members of previously separated subgroups by moving towards a stationary subgroup of hyaenas; leaders at reunions were followed by one or more other hyaenas in the procession that subsequently also joined the new subgroup.

Spotted hyaenas are long-lived animals that reside in complex female-dominated societies, called clans, which may contain 90 or more individuals that defend a common territory (Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012; Kruuk, 1972). Virtually all males permanently disperse from their natal clans after puberty, but females are philopatric (East & Hofer, 2001; Höner et al., 2007; Mills, 1990; Smale, Nunes, & Holekamp, 1997). Clans contain one to several matrilines of adult females and their offspring, as well as one to several adult immigrant males (Frank, 1983). Clans are structured by fission–fusion dynamics; individuals travel, rest and forage alone or in small subgroups that change membership roughly every hour (Smith et al., 2008). Individuals actively join subgroups containing preferred social and sexual partners (Holekamp, Cooper et al., 1997; Smith, Memenis, & Holekamp, 2007; Szykman et al., 2001).

Here we first describe the social and ecological contexts during which hyaenas join new subgroups alone or collectively. Then we ask which form of leadership best characterizes hyaena leader–follower relationships prior to reunions. Leadership in nonhuman animals has historically been categorized as one of two forms: (1) 'personal leadership' (also called 'unshared' or 'despotic leadership') where one or two dominant individuals lead the group by imposing power upon others (Mech, 1970; Rasa, 1987; Schaller, 1963; Watts, 2000) and (2) 'distributed leadership' (also called 'shared' or 'democratic leadership', Conradt & Roper, 2005, 2007) for cases in which leadership roles are equally likely across all group members. However, we find categorizing species as personalized or distributed as problematic because this dichotomy largely depends upon the numbers of individuals sharing a particular attribute (e.g. old or dominant) currently present in the group relative to the numbers of possible leaders at the time of sampling. For example, if elders typically lead in a group with few elders, then this scheme would characterize a species as having personalized leadership. However, if due to stochastic processes alone, that same group in a different sampling period had a large number of elders, then using the traditional dichotomy, this same species would be characterized as having distributed leadership. This traditional scheme is particularly problematic for drawing meaningful conclusions at the species level, and for making evolutionary inferences across taxa, because these definitions depend upon ratios of actual to potential leaders within the group at the time of sampling.

To avoid problems associated with this traditional approach, here we propose a novel, alternative scheme for leadership categorization that depends on whether or not leadership is based on specific traits of individual group members. Attribute-based leadership can be explained by traits such as sex, age class and dominance status. This new framework allows for variable numbers of attribute-based leaders in a group; their numbers will vary with group composition. The evolutionary and cognitive relevance of these categories is much clearer than with the 'personal' versus 'distributed' scheme. Furthermore our scheme should permit development of stronger, mechanistically inspired hypotheses. Thus, if hyaena leadership is best characterized as attribute based, then the tendency for an individual to assume the role of a leader should best be explained by the attributes of individuals (e.g. relative rank within a subgroup, age or tenure, sex, physiological state (hunger level or reproductive state)) when they make decisions regarding whether or not to join other subgroups.

Theory predicts that group travel decisions should emerge from localized interactions (Camazine et al., 2003; Couzin & Krause, 2003). However, the mechanisms that promote followership remain unclear (Petit & Bon, 2010; Ramseyer, Petit, & Thierry, 2009). Therefore, we also inquired whether hyaena leadership is active or passive. If hyaenas rely upon active leadership, then leaders should communicate with followers (e.g. greet them or direct vocal, olfactory or acoustic signals towards them) or coerce them (e.g. direct aggression towards them) into following. If hyaenas use passive leadership, then following should occur without overt communication or coercion.

Group decision-making theory predicts that, whereas members of fission–fusion societies should reduce conflicts of interest by allowing individuals with different interests to separate temporarily from one another, subsequent reunions should provoke conflict (Aureli & Schaffner, 2007; Conradt & Roper, 2005). Although hyaenas do greet former opponents to reconcile after fights (Colmenares, Hofer, & East, 2000; Wahaj, Guse, & Holekamp, 2001), they rely most heavily upon dispersive conflict resolution to prevent escalated aggression (Smith et al., 2008). However, the extent to which subsequent reunions generate conflict among hyaenas is unknown. We therefore inquired whether reunions promote conflict among clan-mates, and whether greetings mitigate this conflict at reunions; greetings are affiliative interactions that occur when two hyaenas stand parallel to one another and sniff each other's anogenital region (East, Hofer, & Wickler, 1993; Smith et al., 2011). Because access to food directly determines reproductive success (Holekamp, Smale, & Szykman, 1996), to understand the potential fitness consequences of conflict at reunions, here we also assessed whether reunions at kills were more likely to be characterized by conflict than were reunions occurring away from food. Among spotted hyaenas, feeding competition is often very intense (Frank, 1986; Kruuk, 1972; Mills, 1990; Smith et al., 2008),