



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



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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.

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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, Cowlshaw, 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 ‘consensus 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

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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, Strelhoff, 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 matrilineal lines 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),

with the highest rates of aggression at ungulate kills (Smith et al., 2007; Wahaj & Holekamp, 2006). Finally, we place our results in a broader context by reviewing the general patterns and mechanisms of leadership for mammals.

METHODS

Study Site and Subjects

Starting in June 1988, we monitored members of a large clan of spotted hyaenas in the Masai Mara National Reserve, Kenya. Here we focus on all reunions observed from 1996 to 2000 because social ranks (Smith et al., 2011) and territory boundaries (Boydston, Morelli, & Holekamp, 2001) were stable throughout this period. Data on leadership at reunions were available from 1996 to 1997. We identified clan members individually by their unique spots and sexed them based on the morphology of the erect phallus (Frank, Glickman, & Powch, 1990).

We estimated ages (to ± 7 days) of cubs upon first observing them above ground (Holekamp et al., 1996). Hyaena cubs live at dens for their first 8–12 months (Boydston, Kapheim, Van Horn, Smale, & Holekamp, 2005; Hofer & East, 1993; Mills, 1990). We considered cubs independent of dens when they were found more than 200 m from the current communal den on at least four consecutive occasions; this occurred at around 9 months of age in our study population (Boydston et al., 2005). Females were considered adults at 36 months, or at their first known date of conception, whichever occurred first, and all immigrant males were also considered adults (Van Horn, McElhinny, & Holekamp, 2003). Adult females were classified based on their lactation status (lactating or nonlactating) and parity (whether or not they had previously given birth). We focused on den-independent subadults and adults; hyaenas in these life history stages often travel alone and are capable of initiating reunions (Smith et al., 2008).

We determined the social rank of each individual hyaena based on outcomes of dyadic agonistic interactions; all adult females were dominant to all immigrant males (Holekamp & Smale, 1993; Smale, Frank, & Holekamp, 1993). Natal hyaenas attain positions in the dominance hierarchy directly below those of their mothers (Engh, Esch, Smale, & Holekamp, 2000). Subadults firmly establish rank positions relative to those of adult females and immigrant males in their clan by roughly 18 months of age (Smale et al., 1993). Once established, social rank relationships remain stable across contexts (Frank, 1986; Smith et al., 2011).

Measures of absolute and relative social rank were both used to inquire whether a hyaena's social status predicted its leadership role. We assigned each individual a social rank in the clan's linear dominance hierarchy, with the highest possible rank being 1, for each year of the study. We also assigned a relative rank position to each hyaena in each travelling subgroup as: (number of companions subordinate to that hyaena in the current subgroup)/(total number of companions in the current subgroup).

As a proxy for current hunger level, we assigned a 'fatness index' value to each individual in each subgroup on a scale from 1 (gaunt) to 4 (obese). This measure reflects recent food intake and is similar to 'belly scores' used for other carnivores (Caro, 1994; Pusey & Packer, 1994); detailed notes on body condition were available from 1996 to 1997.

Behavioural Data Collection

We conducted daily behavioural observations using our field vehicles as mobile blinds; we initiated an observation session each time we encountered one or more hyaenas separated from other clan members by at least 200 m; hyaena subgroups were typically

separated by at least 1 km (Smith et al., 2008). We assigned a context to each observation session depending on whether it occurred at a den occupied by cubs, when hyaenas were actively hunting prey, at a kill site with one or more hyaenas feeding on a fresh ungulate carcass, when hyaenas were mating, during conflicts with lions or during territorial border patrols (e.g. scent marking at territory boundaries; for additional details, see Boydston et al., 2001; Smith et al., 2008). Sessions included here lasted from 10 min to several hours and ended when we left the individual or subgroup.

We recorded the identities of all hyaenas present at the start of each session and those of individual hyaenas arriving and leaving during the session. In the minutes before two subgroups merged, we observed both the arriving and joined subgroups; initiation of the reunion was determined by patterns of approach. That is, subgroup reunions were initiated by either a single hyaena travelling alone, or collectively by two or more hyaenas travelling together, which joined a stationary subgroup. To be included in the data set comparing pre- and post-fusion behaviours, all members of both original and joining subgroups had to be clearly observable for at least 5 min before and 5 min after their reunion.

Leadership and Behavioural Interactions at Reunions

From 1996 to 1997, subgroup leaders were identified when one hyaena was travelling at the vanguard of a procession prior to a reunion. Leaders at reunions were those individuals that first initiated contact with members of the joined subgroup. Followers travelled behind and in the same direction as the leader. Followers arrived at the joined subgroup within 1 min of the leader initiating the reunion. To quantify information exchanged between leaders and followers, we recorded all visual (e.g. bristled tails, looking back), acoustic (vocalizations) and olfactory signals (e.g. scent marking, social sniffing) exchanged among members of each arriving subgroup. We did this during the 5 min before reunions with another subgroup, referred to as the pre-fusion period. The 5 min after a reunion were referred to as the post-fusion period.

We recorded all occurrences of greetings, aggression and appeasements using all-occurrence sampling (Altmann, 1974). We classified the first social interaction each arriving hyaena had with one or more members of the joined subgroup, regardless of which animal initiated the behavioural exchange, as (1) an affiliative interaction (e.g. greetings, nonaggressive approach within 1 m, sniffing or grooming), (2) an aggressive interaction (e.g. lunge, snap, bite, chase, displace, push, stand over and intentional movement to bite), or (3) unsolicited appeasement (e.g. head bobbing, submissive posture, carpal crawling and open-mouth appeasement that occurs prior to, or in the absence of, aggression). If none of these interactions occurred, arriving hyaenas were assigned to a fourth category: no obvious interaction.

Following Aureli and Schaffner (2007), we calculated the baseline hourly rates at which each subject greeted with or initiated aggression towards other members of their original subgroup during the pre-fusion period. We compared these rates to those for the same subjects during the post-fusion period. We also calculated hourly rates of behaviours exchanged between joined and joining hyaenas by dividing the hourly rates for each measure by the number of potential partners available in one and both subgroups, respectively. We quantified the tendency for hyaenas to initiate social interactions at reunions, and assessed whether reunions at kills were more likely to be characterized by conflict than were reunions occurring away from food. Finally, we asked whether greetings mediate conflict at reunions by assessing whether focal hyaenas were subsequently less likely to fight during the post-fusion period at reunions when they greeted with hyaenas from

whom they were previously separated than at reunions when they failed to greet.

Statistical Analyses

We used Statistica 6.1 (StatSoft, Inc., Tulsa, OK, U.S.A.) to analyse data failing to meet assumptions of normality and/or homoscedasticity of variances. We used Mann–Whitney *U* tests to compare means for two independent groups and Kruskal–Wallis tests to compare means among more than two independent groups. We used Wilcoxon signed-ranks tests and Friedman's ANOVA for repeated measures when comparing means of two or more than two dependent groups, respectively. We considered differences to be statistically significant at $\alpha < 0.05$. We corrected for multiple testing using the sequential Bonferroni adjustment (Rice, 1989) and report *P* values in their adjusted form. We report means \pm SE.

We used generalized linear mixed models (GLMM) in lme4 (Bates & Maechler, 2010) in R v.2.6.2 (R Foundation for Statistical Computing, Vienna, Austria) to model two binary response variables. First, we assessed how social and ecological contexts influenced the extent to which clan-mates were found joining subgroups along with other travellers (binary response: joined together with clan-mates (yes) or joined on their own (no)). Second, we modelled the tendencies for hyaenas to assume the position of leader (binary response: lead (yes) or follow (no)) in each procession resulting in a reunion with clear leadership roles.

We sequentially entered and dropped all potential explanatory terms, including interaction terms, and deemed the candidate model with the smallest Akaike's information criterion (AIC) to be best (Burnham & Anderson, 2002). No strongly intercorrelated variables were retained in final models ($r^2 \leq 0.31$). We obtained statistics for terms removed from our best models by adding each term to minimal models. We entered the identity of each hyaena as a random effect to avoid potential pseudoreplication, as well as to assess the extent to which leaders were consistent across travelling parties. We tested the effect of hyaena identity in each model using likelihood ratio tests (Pinheiro & Bates, 2000).

To assess whether hyaenas lead or follow, we used permutation-based statistics to compare the GLMM results from our data to those generated from null models for two sets of analyses: (1) for the full data set of den-independent subadults and adults and (2) for a reduced data set, restricted only to adults and den-independent subadults that were no longer nursing. The leadership data were analysed using permutation tests for two reasons. First, this approach rules out possible effects of sampling biases in the data collection (e.g. some individuals are more likely to be observed than others). Second, this modelling approach explicitly controls for the possibility that subgroup size of travelling parties and, thus the likelihood that an individual was in a leadership position, might be confounded by travelling group size.

We simulated data by randomly distributing leadership positions amongst all subjects observed at reunions. These simulations broke down the possibility of an uneven distribution of individuals of a certain type occupying travelling parties of certain sizes. Specifically, group membership of travelling parties was retained from our original data set and the individual who was the leader was permuted 10 000 times. Then, we ran regression models on the permuted versions of the data (e.g. one GLMM regression model for each of the 10 000 randomized data sets). To calculate *P* values, we compared the regression estimate for the best-fit model based on our data to the distribution of estimates for the permuted data, as suggested by Croft, James, and Krause (2008). Specifically, model estimates from our data set were considered statistically significant when their values were outside the range of 95% confidence intervals (CIs) of estimates constructed from simulated data. The

effect of party size on the tendency to lead at reunions was assessed by entering travel subgroup size into each model.

RESULTS

Size and Contexts of Travelling Parties at Reunions

From 1996 to 2000, during 4217 observation hours, we recorded 5990 arrivals of subgroups (reunions) involving 133 arriving individuals. The majority (79.5%) of reunions ($N = 4766$ reunions) were initiated by one hyaena arriving on his/her own, with a mean arrival party size of only 1.4 ± 0.01 hyaenas.

Whether or not hyaenas arrived with others or alone varied with the current social and ecological circumstances (Fig. 1a). Specifically, individuals arriving at dens or joining hunting parties were significantly less likely to arrive with companions than to arrive on their own (den: -0.247 ± 0.068 , $Z = -3.621$, $P = 0.0003$; hunting: -0.547 ± 0.221 , $Z = -2.474$, $P = 0.013$; Fig. 1a). In contrast,

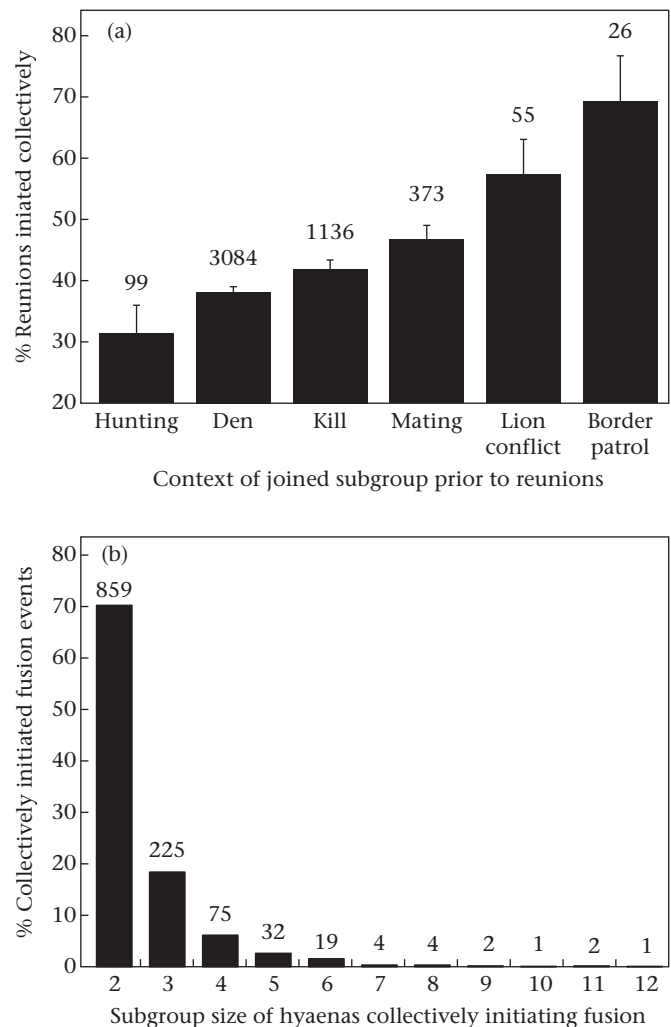


Figure 1. (a) Mean percentage \pm SE of reunions initiated collectively (rather than alone), on average, by each of 133 individual hyaenas as a function of the social and ecological contexts experienced at reunions (see Methods for definitions). Sample sizes above bars represent the total number of reunions for each context. Reunions not shown here occurred in the context 'other' ($N = 268$ collective and 943 alone reunions), and on six occasions, hyaenas arrived on their own at clan wars. (b) Percentage of all collective reunions (involving at least two hyaenas arriving together) as a function of the party size of each travelling subgroup. Sample sizes above bars represent the number of collective reunions observed for each party size.

hyaenas were more likely to arrive with clan-mates (than on their own) when joining others to participate in group defence of shared resources during conflicts with lions (0.532 ± 0.240 , $Z = 2.212$, $P = 0.027$) and territory border patrols (1.047 ± 0.352 , $Z = 2.978$, $P = 0.003$). Reunions were just as likely to involve the arrival of lone individuals as subgroups composed of multiple hyaenas at kill sites (-0.090 ± 0.083 , $Z = -1.086$, $P = 0.278$) and at sessions involving mating (0.104 ± 0.110 , $Z = 0.943$, $P = 0.345$).

Groups of multiple hyaenas ($N = 1224$ reunions, range 2–12 hyaenas) arriving to join existing subgroups were composed of 2.5 ± 0.03 hyaenas (Fig. 1b). Some individuals were consistently more likely to arrive at sessions collectively than were others (likelihood ratio test for random effect of individual: $\chi^2_1 = 88.3$, $P < 0.0001$). Collective reunions were also more common in some years than in others (year: $\chi^2_1 = 6.13$, $P = 0.013$).

Modelling Factors Distinguishing Leaders from Followers at Fusion

From 1996 to 1997, in the 675 reunions for which hunger level was known for all subjects, only one 'well-fed' hyaena (a follower) ever arrived with companions during subgroup fusion. Our finding that all of the remaining participants were neither fat nor obese (99.9% of records) suggests that 'well-fed' hyaenas are rarely accompanied by conspecifics at subgroup fusion. Because 'well-fed' hyaenas virtually always joined subgroups on their own, we lacked the statistical power to model effects of hunger on leadership roles. We therefore focused on the full data set (1996 to 2000) to identify which of the remaining predictor variables best distinguishes leaders from followers at reunions.

We could clearly distinguish between leaders and followers in 271 travelling precessions prior to reunions. Hyaena identity failed to improve the fit of our best model (likelihood ratio test: $\chi^2_1 = 0.371$, $P = 0.543$; Table 1). That is, no specific individual(s) consistently led all reunions during this 5-year study. However, not all individuals were equally likely to lead. Instead, as predicted by the attribute-based leadership hypothesis, leadership was biased towards individuals belonging to specific age and sex categories (e.g. Fig. 2). Specifically, all adult females in the clan were habitual leaders. In contrast, subadults and immigrant males habitually assumed roles as followers during most collective reunions.

Within each travelling subgroup, the highest-ranking member typically assumed the vanguard position prior to reunions, as reflected by the high relative social rank of leaders (relative social rank: 1.308 ± 0.259 , $Z = 5.050$, $P < 0.00001$; Table 1, Fig. 3). Although the relative rank of each hyaena within a travelling subgroup predicted its leadership role, a hyaena's overall social rank in the clan's hierarchy did not (0.014 ± 0.010 , $Z = 1.513$, $P = 0.130$). Age class and sex interacted to affect whether hyaenas emerged as leaders ($P < 0.007$; Table 1). That is, although subadult and adult females were more likely to lead than were subadult or adult males, the bias towards leadership by females was more extreme for adults (sex: 1.904 ± 0.389 , $Z = 4.898$, $P < 0.00001$) than for subadults (sex: 0.968 ± 0.454 , $Z = 2.130$, $P < 0.001$). Interestingly,

lactating females were significantly more likely to assume leadership roles than were nonlactating females (0.625 ± 0.296 , $Z = 2.110$, $P < 0.004$; Table 1, Fig. 3). Parity (0.185 ± 0.208 , $Z = 0.892$, $P = 0.372$), age class (-0.010 ± 0.019 , $Z = -0.554$, $P = 0.580$) and tenure in the clan (-0.002 ± 0.003 , $Z = -0.483$, $P = 0.629$) failed to improve the fit of our best model.

We next inquired how the lactation status of focal females ($N = 16$) influenced the age–sex classes of their followers. After correcting for the number of individuals within each age class available to follow focal adult females at reunions, we found that the extent to which focal females were followed by subadults, adult females or immigrant males varied significantly for both lactating leaders (Friedman's ANOVA: $F_{2,16} = 8.8$, $P = 0.015$) and nonlactating leaders ($F_{2,16} = 11.3$, $P = 0.003$). Lactating females were significantly more likely to be followed by subadults than by adults of either sex (Wilcoxon signed-ranks tests: $Z = -2.90$, $P = 0.012$, for both sexes, after correcting for multiple testing). Immigrant male and adult female followers of lactating females were equally likely per opportunity to follow ($Z = -0.978$, $P = 0.327$). When subadults followed lactating females at reunions, females were followed on average, by 1.2 ± 0.1 offspring that were still nursing, a value that was significantly greater than the numbers of weaned subadults that followed (0.3 ± 0.1 hyaenas, $Z = -3.621$, $P = 0.0003$). In contrast, nonlactating females were followed by immigrant males and subadults to similar extents ($Z = -1.079$, $P = 0.280$). After correcting for multiple testing, subadults and immigrant males were both significantly more likely than were adult females to follow nonlactating females ($Z = -2.803$ and -3.059 , $P = 0.010$ and 0.006 , respectively).

Given that lactating females were often followed by dependent offspring, we next restricted our data set to only weaned subadults and adults to rule out the possibility that the detected bias in leadership by lactating adult females was simply due to followership by den-independent, but still nursing, offspring. Interestingly, our findings remained robust even after we excluded nursing subadults as potential followers. That is, relative rank, sex, age class and lactation remained statistically significant predictors of whether a hyaena assumed the role of leader prior to a reunion even in this reduced data set ($P < 0.02$ for all variables; Table 2).

Mechanisms Promoting Leadership at Reunions

Followers ($N = 76$ hyaenas) always travelled in the same cardinal direction as leaders, and, on average, remained 16 ± 2 m behind leaders during the 5 min before reunions (median = 20 m, range 1–160 m). However, we found no evidence that leaders actively communicated with or coerced followers; instead our data suggest that hyaenas rely upon passive leadership. Leaders failed to consistently raise or bristle their tails, glance back at followers, deposit scent marks or vocalize prior to initiating subgroup fusion. On only on one occasion did an adult female scent-mark and paw the ground immediately before leading her companions to join a new subgroup.

Table 1
Independent variables predicting whether focal hyaenas would be leaders at reunions

Coefficients	Estimate \pm SE	Estimate 95% CI	Z	P
Travelling subgroup size	-0.375 ± 0.068	-0.351 to -0.325	-5.490	<0.00001
Relative social rank	1.308 ± 0.259	-0.579 to 0.498	5.050	<0.00001
Lactating	0.625 ± 0.296	-0.547 to 0.464	2.110	<0.004
Age class (adult)	0.674 ± 0.396	-0.436 to 0.509	1.703	<0.00001
Sex (female)	0.829 ± 0.409	-0.581 to 0.585	2.028	<0.003
Age class * sex	1.110 ± 0.530	-0.736 to 0.896	2.094	<0.007

$N = 103$ unique hyaenas ($N_M = 53$, $N_F = 50$) at 271 unique reunions as subadults ($N_M = 30$, $N_F = 24$) and adults ($N_M = 23$, $N_F = 33$). Intercept: -1.581 ± 0.391 ; $Z = -4.041$, $P < 0.00005$.

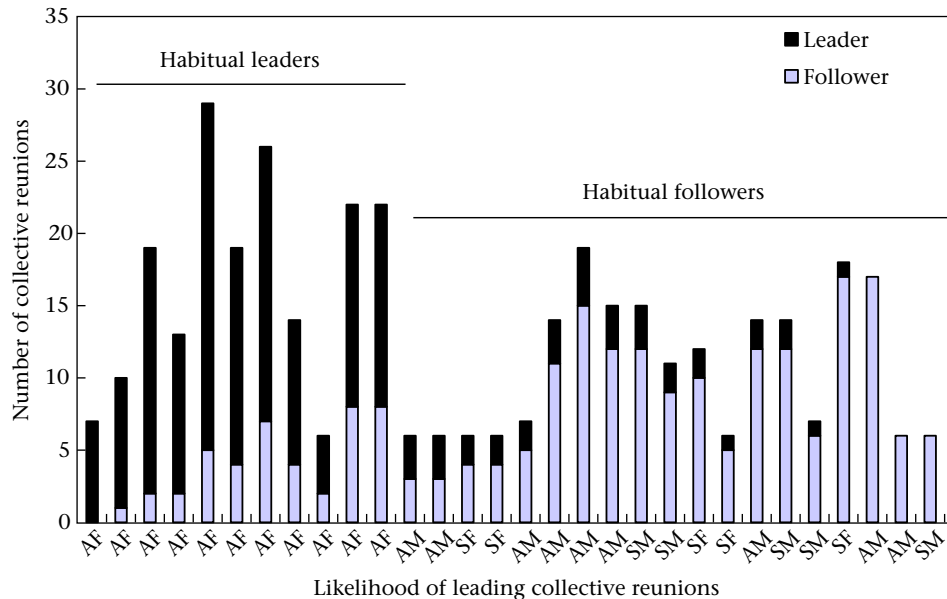


Figure 2. A representative cross-section of habitual leaders ($N = 11$ hyaenas that led more often than they followed) and habitual followers ($N = 19$ hyaenas that followed more often than they led) at reunions from 1996 to 1997. Subadult (S) and adult (A) males (M) and females (F) are ordered from the hyaena that assumed a leadership role most often (on the left) to the hyaena that led least often (on the right) during collective reunions in which he/she was involved.

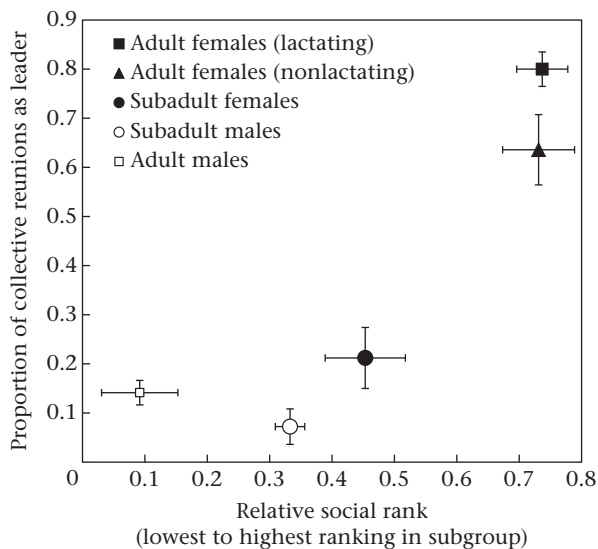


Figure 3. Relationships between hyaenas' relative social rank within subgroups and the proportion of collective reunions in which hyaenas were leaders when they could be assigned to one of the following categories: (1) lactating adult females ($N = 24$), (2) nonlactating adult females ($N = 28$), (3) subadult females ($N = 24$), (4) subadult males ($N = 30$) and (5) adult immigrant males ($N = 23$). Relative social ranks ranged from 0 (the hyaena of the lowest social rank in a travelling subgroup) to 1 (the hyaena of the highest social rank in a travelling subgroup). Mean \pm SE of relative social rank within travelling subgroups (horizontal axis and error bars) and proportion of collective reunions (vertical axis and error bars) are shown for hyaenas belonging to each category.

Leaders tended to greet with clan-mates at lower rates during pre-fusion periods than during post-fusion periods (0.03 ± 0.02 versus 0.30 ± 0.10 greetings per partner per h, respectively), but this difference was not statistically significant (Wilcoxon signed-ranks test: $Z = 1.69$, $P = 0.091$). We found no evidence of coercion. Indeed, leaders were significantly more tolerant of followers during the pre-fusion period than during the post-fusion period (0.13 ± 0.07 versus 0.45 ± 0.19 aggressive attacks per target per h, respectively: $Z = 2.84$, $P = 0.005$). Overall, these results are more

consistent with the passive leadership hypothesis than with the active leadership hypothesis.

Escalated Affiliation and Conflict at Reunions

Unsolicited appeasements, aggression and greetings at reunions

Many of 2824 reunions involved multiple hyaenas joining per reunion. We therefore observed a total of 6484 instances where a focal, newly arriving hyaena ($N = 133$ unique individuals) could potentially interact with one or more members of the joined subgroup. Overall, joining hyaenas varied in their tendencies to participate in specific types of social interaction during the first 5 min after reunions (post-fusion period; Friedman's ANOVA: $F_{3,133} = 253.6$, $P < 0.00001$; Fig. 4). Although many joining hyaenas failed to engage in any obvious social interactions immediately after fusion ($44.2 \pm 1.8\%$ hyaenas per reunion; Fig. 4), arriving hyaenas participated in affiliative interactions much more frequently than in aggression or unsolicited appeasements ($Z \geq 9.11$, $P < 0.00001$ for both). Of the 2418 affiliative interactions at reunions, roughly half of these were greetings (50%, $N = 1121$ greetings). Initial interactions at reunions were also more often characterized by unsolicited appeasement than by aggression ($Z = 3.17$, $P = 0.003$).

Hourly rates of aggression and greetings at reunions

On average, we observed a total of 41 ± 2 pre- and post-fusion periods per subject ($N = 148$ individuals belonging to 2824 joined subgroups). Each focal joined hyaena was observed, on average, for a total of 6.8 ± 0.4 h during pre- and post-fusion periods. On average, 2.8 ± 2.6 hyaenas joined each subgroup (range 1–24 arrivals per post-fusion period).

Based on these data, we compared rates of greetings and aggression among (1) members of joined and joining subgroups before reunions, (2) members of the same subgroup before and after reunions, and (3) members of joined and joining subgroups after reunions. Overall, hourly rates of greetings varied among the categories of subjects during the pre- and post-fusion periods (Friedman's ANOVA: $F_{2,148} = 101.8$, $P < 0.00001$; Fig. 5a). As

Table 2
Independent variables predicting whether focal weaned hyaenas would be leaders at reunions

Coefficients	Estimate±SE	Estimate 95% CI	Z	P
Travelling subgroup size	-0.362±0.073	-0.289 to -0.279	-4.927	<0.00001
Relative social rank	1.489±0.302	-0.619 to 0.596	4.929	<0.00001
Age class (adult)	1.705±0.396	-0.492 to 0.478	4.302	<0.00001
Sex (female)	1.822±0.363	-0.527 to 0.489	5.023	<0.00001
Lactating	0.555±0.311	-0.471 to 0.531	1.787	<0.018

$N = 83$ unique weaned hyaenas ($N_M = 41$, $N_F = 42$) at 216 unique reunions as subadults ($N_M = 18$, $N_F = 15$) and adults ($N_M = 23$, $N_F = 33$). Intercept: estimate = -2.783 ± 0.475 , $Z = -5.854$, $P < 0.00001$; adult*sex: estimate: 0.461 ± 0.534 , CI: -0.914 to 1.227 , $Z = 0.864$, $P = 0.277$.

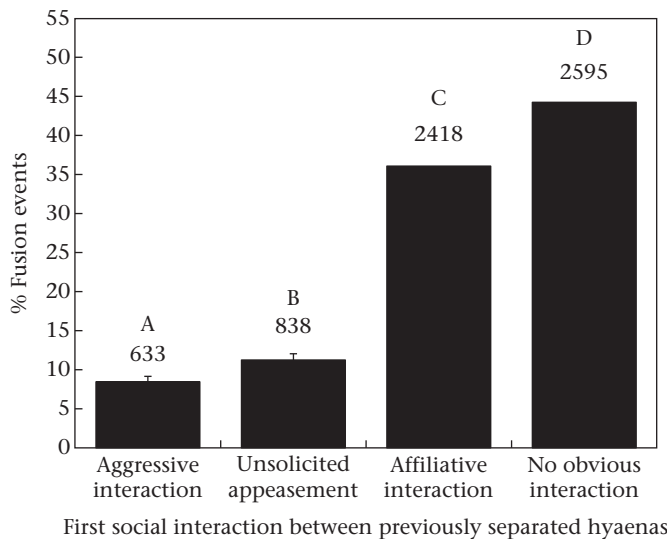


Figure 4. Mean \pm SE proportion of reunions in which arriving hyaenas ($N = 133$) first engaged in an aggressive interaction ($N = 633$), an affiliative interaction ($N = 2418$), or an unsolicited appeasement ($N = 838$) with at least one member of the joined subgroup. In the remaining cases, these same individuals were not involved in any obvious social interaction ($N = 2595$) within the first 5 min after joining that subgroup.

predicted, hyaenas belonging to joined subgroups greeted with arriving hyaenas at higher hourly rates per opportunity than with members of their original subgroup during either the pre-reunion or post-fusion periods (Wilcoxon signed-ranks test: $Z = 9.36$ and 8.51 , respectively, $P < 0.00001$ for both; Fig. 5a). In contrast, members of the original (pre-fusion) subgroup greeted with one another at lower hourly rates after than before new arrivals joined their subgroup ($Z = -2.84$, $P = 0.008$; Fig. 5a).

As with greetings, hourly rates of aggression also differed between pre- and post-fusion periods (Friedman's ANOVA: $F_{2,148} = 37.8$, $P < 0.00001$; Fig. 5b). Similarly, hyaenas belonging to joined subgroups fought with arriving hyaenas at higher hourly rates than with members of their original subgroup during either the pre-fusion or post-fusion period (Wilcoxon signed-ranks test: $Z = 5.26$ and 7.01 , respectively, $P < 0.00001$ for both). The hourly rate at which members of the original (pre-reunion) subgroup attacked one another was also significantly higher during the post-reunion period than during the pre-reunion period ($Z = 4.27$, $P = 0.00002$; Fig. 5b). Thus, reunions promoted conflict among hyaenas previously found in different subgroups (inter-subgroup aggression) as well as among animals that previously belonged to the same subgroups (intra-subgroup aggression).

Greetings Mitigate Conflict at Reunions

Arriving hyaenas were significantly more likely to be the individuals responsible for initiating ($70 \pm 3\%$ of greetings) rather

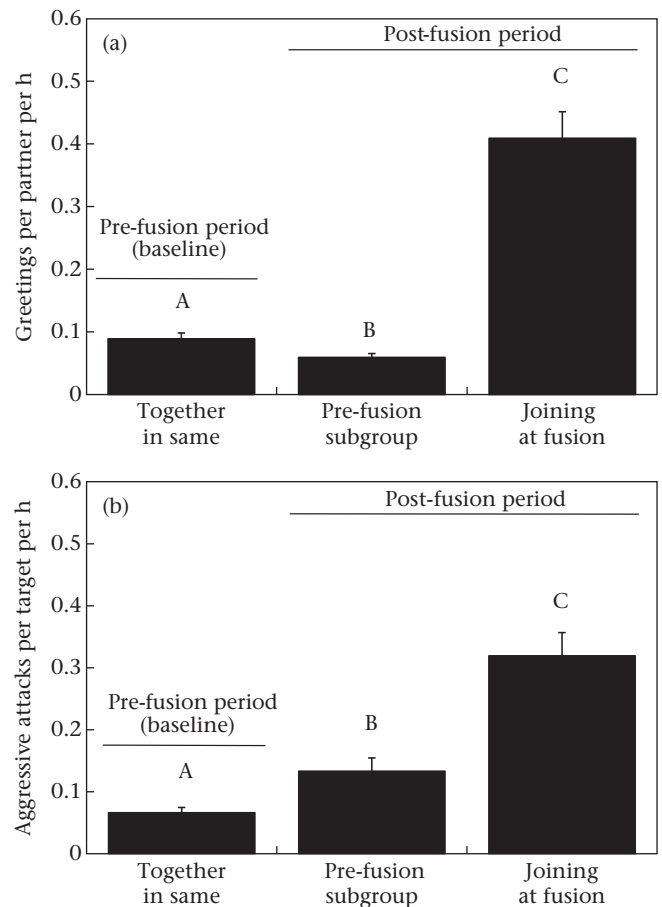


Figure 5. Mean \pm SE hourly rates of (a) greetings and (b) aggressive acts exchanged during the post-fusion period among individuals that were together in the same subgroup before and after arriving hyaenas joined the subgroup, as well as rates of behaviours exchanged with arriving hyaenas after the fusion event ($N = 148$ focal hyaenas belonging to 2824 joined subgroups).

than receiving greetings at reunions (Wilcoxon signed-ranks test: $Z = 3.38$, $N = 69$ hyaenas, $P = 0.0007$). Arriving hyaenas were also responsible for initiating aggression at reunions. That is, when fights occurred at reunions, newly arriving hyaenas were significantly more likely to start those fights than were members of joined subgroups ($69 \pm 4\%$ of fights started by newly arriving hyaenas; $Z = 4.67$, $N = 70$ hyaenas, $P < 0.00001$).

Focal individuals that were involved in the highest hourly rates of greetings were also the individuals that were involved in the highest hourly rates of aggression at reunions (Wilcoxon signed-ranks test: $Z = 2.63$, $N = 148$ hyaenas, $P = 0.008$). Thus, hyaenas exhibited interindividual variation in the extent to which they socialized at reunions. However, arriving individuals rarely participated in both greetings and fights during the same post-fusion

period; in only 41 of 2824 reunions did an arriving hyaena both fight and greet one or more members of its new subgroup. During the post-fusion period at reunions for which arriving hyaenas both fought and greeted with newly joined hyaenas, arriving hyaenas were more likely to direct greetings and attacks towards different group-mates than towards the same individuals (Wilcoxon signed-ranks test: $Z = 1.380$, $N = 28$ hyaenas, $P = 0.168$). Arriving hyaenas that participated in both forms of social interactions at the same reunions were equally likely to first greet ($45 \pm 9\%$ of reunions) or fight a member of the joined subgroup ($55 \pm 9\%$ of reunions; $Z = 0.548$, $N = 28$ hyaenas, $P = 0.582$). As predicted, feeding competition was a large source of conflict at reunions. Food was present at significantly more aggressive reunions ($34 \pm 1\%$ of reunions) than at affiliative reunions ($21 \pm 1\%$ of reunions; Wilcoxon signed-ranks test: $Z = -5.05$, $N = 51$ hyaenas, $P < 0.0001$).

As predicted by the conflict mitigation hypothesis, arriving hyaenas whose first social interaction at reunions was a greeting were more protected from subsequent aggression during the post-fusion period than were arriving hyaenas that failed to first greet those same conspecifics at reunions on different occasions. Specifically, arriving hyaenas received significantly less aggression during the post-fusion periods at sessions when they first initiated a greeting with a newly joined group member than at sessions when their first social interaction did not involve a greeting (Wilcoxon signed-ranks test: $Z = 6.731$, $N = 75$ hyaenas, $P < 0.00001$; Fig. 6). Thus, an individual hyaena was, on average, 7.7 times less likely to fight with an individual in its new subgroup when they greeted conspecifics than when they failed to greet.

Forms and Mechanisms of Leadership during Group Travel in Mammalian Groups

Overall, forms of leadership during group travel are well documented for 52 species of mammals, including spotted hyaenas (Table 3). The vast majority (89%) of species are best characterized by attribute-based leadership ($N = 47$ species; Fig. 7a). Only 9% of species ($N = 5$ species), exhibit a non-attribute-based pattern of

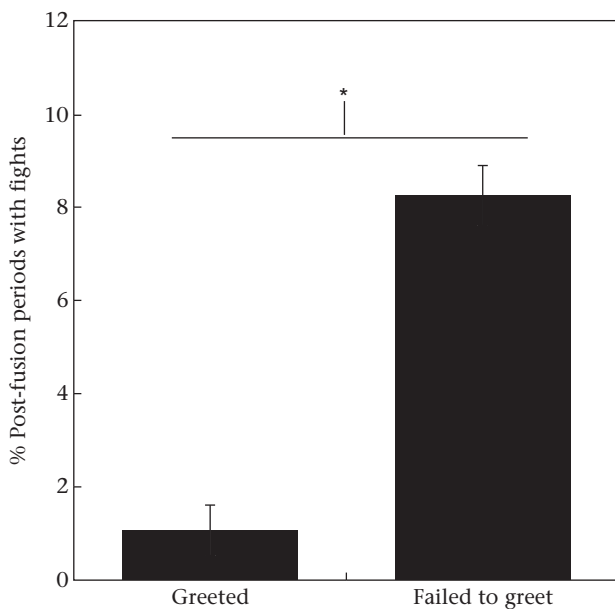


Figure 6. Mean \pm SE percentage of sessions in which arriving hyaenas ($N = 75$ focal individuals) received aggression when they first initiated a greeting with a newly joined member of a stationary subgroup, or when the first social interaction of those same arriving hyaenas failed to involve a greeting at reunions.

leadership. Among all species characterized by attributed-based leadership, leaders were always adults (Table 3). Of these species, 39 species (83%) showed a sex bias. Sex biases were largely due to conspecifics following females ($N = 28$ species; 71%); in only 11 species (28%) did conspecifics primarily follow adult males. Among species biased towards following adult females, seven of these species (25%) followed lactating females most often. Surprisingly, leaders were of high social rank in only eight species.

Mechanisms used by leaders to recruit followers during group travel are known for 49 of the 52 species reviewed here (Table 3, Fig. 7b). Primarily passive mechanisms, defined as no obvious signals to recruit followers, are used by only 10 of these species. Most (80%, $N = 39$) species actively recruit followers. Coercion via overt aggression, however, was rarely used. Coercion was limited to primates and ungulates, particularly within the context of consortships. For example, male chimpanzees, *Pan troglodytes*, hamadryas baboons, *Papio hamadryas*, musk oxen, *Ovibos moschatus*, Przewalski horses, *Equus ferus przewalskii*, and plains zebra, *Equus quagga*, sometimes use aggression to herd potential mates, forcing females to move in a particular direction (Table 3). Interestingly, however, all of these species primarily rely upon mechanisms other than coercion to promote followership (Fig. 7b). Most active recruitment involves signals targeting one or more sensory modalities. Acoustic (67%), visual (56%), tactile (23%) and/or olfactory (18%) communication occur in the 39 species producing one or more signals to recruit followers. Interestingly, olfactory signals are limited to social carnivores.

DISCUSSION

Evidence for Attribute-based Leadership

Overall, attribute-based leadership is by far the most common pattern of leadership among mammals. Our findings have important evolutionary implications suggesting that leadership may be a trait subject to selection. Interestingly, roles may be occupied by various group members across time when flexibility allows groups to increase travel efficiency. Taken together, our findings support the emerging view that an individual's motivational state, sex, relative social status and age class profoundly shape his/her leadership roles during group travel.

These patterns are also consistent with the prediction that, when group members vary individually, natural selection is expected to favour leadership by those group members in a given context possessing the most accurate knowledge (Ben-Yashar & Nitzan, 1997) or most pressing physiological needs (e.g. Rands et al., 2003). Indeed, female elders, presumably with the most local knowledge, often enlist more followers than do young, naive individuals in mammals such as lions, *Panthera leo* (Schaller, 1972), Verreaux's sifakas, *Propithecus verreauxi* (Trillmich, Fichtel, & Kappeler, 2004), and killer whales, *Orcinus orca* (Brent et al., 2015). Philopatric adult female hyaenas likely possess greater social and ecological knowledge than do subadults or adult males who have recently immigrated from neighbouring social groups.

Hyaenas learn socially, and subadults often acquire knowledge from adults (e.g. hunting skills, Holekamp et al., 1996). Although adult female hyaenas in the current study were followed most often, followership is clearly based on multiple factors in addition to local knowledge. For example, immigrant males following sexually receptive females primarily do so because they seek mating opportunities (e.g. Szykman et al., 2001). Lactation status was also a better predictor of followership than was the age of adult females. Naturally, den-independent, but still nursing, subadults sometimes follow their mothers to seek nourishment. Interestingly, however, the tendency for lactating females to lead most often was

Table 3
Attributes and mechanisms of leadership during group travel in mammals

Species	Attributes of most leaders ^a	Mechanisms to recruit followers	Sources
Apes (<i>N</i> =3 species)			
Humans, <i>Homo sapiens</i>	Multi-faceted, most=Adult (M)	Acoustic, Tactile, Visual and Coercion	Dyer, Johansson, Helbing, Couzin, and Krause (2009); Firth (1972); Van Vugt (2006); Moussaid, Perozo, Garnier, Helbing, and Theraulaz (2010)
Chimpanzees, <i>Pan troglodytes</i>	High rank, Adults (M)	Visual (glance back and pause); Males=Coercion	Goodall (1986); Hockings, Anderson, and Matsuzawa (2006)
Mountain gorillas, <i>Gorilla beringei beringei</i> ^b	Alpha Adult (M) ^c	Acoustic and Visual (vocal, glance back, pause)	Schaller (1963); Stewart and Harcourt (1994); Watts (2000)
Monkeys (<i>N</i> =23 species)			
Hamadryas, <i>Papio hamadryas</i> ^b	Adults (M)	Visual (glance back); Males=Coercion	Kummer (1968); Sigg and Stolba (1981)
Chacma baboons, <i>P. ursinus</i>	Most studies=Adult M (variable across studies)	Acoustic and Visual (vocal, glance back and pause)	Barrett, Halliday, and Henzi (2006); Byrne, Whiten, and Henzi (1990); Cheney, Seyfarth, and Palombt (1996); King, Douglas, Huchard, Isaac, and Cowlishaw (2008); Stueckle and Zinner (2008)
Yellow baboons, <i>P. cynocephalus</i>	High rank, Adults (M)	Visual (gesture)	Altmann (1979); Norton (1986); Rhine (1975)
Japanese macaques, <i>Macaca fuscata</i>	High rank, Adults	Passive	Jacobs, Watanabe, and Petit (2011); O. Petit (personal communication, 29 November 2014)
Rhesus macaques, <i>M. mulatta</i>	High rank, Adults (M)	Acoustic and Visual (vocalize, glance back, pause)	Reinhardt, Reinhardt, and Houser (1987); Sueur and Petit (2008, 2010)
Tonkean macaques, <i>M. tonkeana</i>	Non-attribute-based	Visual (glance back and pause)	Sueur and Petit (2008, 2010)
Barbary macaques, <i>M. sylvanus</i>	High rank, Adults (M)	Visual (glance back and pause)	Seltmann, Majolo, Schülke, and Ostner (2013)
White-faced capuchin monkeys, <i>Cebus capucinus</i>	Adults (F)	Acoustic and Visual (vocalize, glance back, pause)	Boinski (1993); Leca, Gunst, Thierry, and Petit (2003)
Tufted capuchin monkeys, <i>C. apella</i> ^d	High rank, Adults	Passive	Di Bitetti and Janson (2001)
Geladas, <i>Theropithecus gelada</i>	Adults (F, lactating)	Acoustic (vocalize)	Aich, Moos-Heilen, and Zimmermann (1990); Dunbar (1983)
White-handed gibbons, <i>Hylobates lar</i>	Adults (F, lactating)	Unknown	Barelli, Boesch, Heistermann, and Reichard (2008)
Black-and-white ruffed lemurs, <i>Varecia variegata</i>	Most studies=Adult F (variable across studies)	Acoustic (vocal)	Overdorff, Erhart, and Mutschler (2005); Pereira, Seeligson, and Macedonia (1988) ^e
Ringtailed lemurs, <i>Lemur catta</i>	Adults (F)	Acoustic (vocal)	Jolly (1966); Sauther and Sussman (1993)
Fork-marked lemurs, <i>Phaner furcifer</i>	Adults (F)	Acoustic (vocal)	Charles-Dominique and Petter (1980)
Brown lemurs, <i>Eulemur fulvus rufus</i>	Adults (F, lactating)	Acoustic (vocal)	Erhart and Overdorff (1999); Pereira and Kappeler (1997)
Milne-Edwards' sifakas, <i>Propithecus diadema edwardsi</i>	Adults (F, lactating)	Acoustic (vocal)	Erhart and Overdorff (1999); Kubzdela, Richard, and Pereira (1992)
Indri, <i>Indri indri</i>	Adult (F)	Acoustic (vocal)	Pollock (1979)
Verreaux's sifakas, <i>P. verreauxi</i>	Adults (F)	Acoustic (vocal)	Trillmich et al. (2004)
Squirrel monkeys, <i>Saimiri oerstedii</i>	Adults (F)	Acoustic (vocal)	Boinski (1991)
Saddleback tamarins, <i>Saguinus fuscicollis</i>	Adults (M)	Passive	A. C. Smith (personal communication, 24 November 2014); Smith, Buchanan-Smith, Surridge, and Mundy (2003)
Mustached tamarins, <i>S. mystax</i>	Adults (F)	Passive	A. C. Smith (personal communication, 24 November 2014); Smith et al. (2003)
Black and gold howler monkeys, <i>Alouatta caraya</i>	Adults (M & F)	Acoustic and Visual (vocalize)	V. A. Fernández (personal communication, 25 November 2014); Fernández, Kowalewski, and Zunino (2013)
Black howler monkeys, <i>Alouatta pigra</i>	Adults (F)	Acoustic (vocalize)	Van Belle, Estrada, and Garber (2013)
Carnivores (<i>N</i> =12 species)			
Grey wolves, <i>Canis lupus</i>	Most studies=Alpha Adults (M & F) ^c	Olfactory, Tactile and Visual (greet, social sniff, groom and tail wags)	Mech (1970); Peterson, Jacobs, Drummer, Mech, and Smith (2002); Scott (1965)
Domestic dogs, <i>C. l. familiaris</i>	High-rank, Adults (M & F)	Olfactory and Tactile (greet)	Ákos, Beck, Nagy, Vicsek, and Kubinyi (2014); Bonanni et al. (2010); Scott (1965)
Golden jackals, <i>C. aureus</i>	Adults (M)	Olfactory, Tactile and Visual (greet, social sniff and tail wag)	Macdonald (1979)
Bush dogs, <i>Speothos venaticus</i>	High rank, Adults (M & F)	Olfactory and Tactile (greet, urinate)	Macdonald (1996)
African wild dogs, <i>Lycaon pictus</i>	Most studies=Alpha adults (M & F) ^c	Acoustic, Olfactory, Tactile and Visual (vocalize and greet)	Creel and Creel (2002); Estes and Goddard (1967); Schaller (1972)
African lions, <i>Panthera leo</i>	Adults (F)	Olfactory and Tactile (greet, groom and scent mark)	Schaller (1972)
Meerkats, <i>Suricatta suricatta</i>	Alpha adult (F) ^c	Acoustic (vocalize)	Bousquet, Sumpster, and Manser (2011)
Dwarf mongooses, <i>Helogale parvula</i>	High rank, Adults (F)	Acoustic, Olfactory, Tactile and Visual (vocalize, greet, groom and mark)	Maier, Rasa, and Scheich (1983); Rasa (1977, 1987)
Spotted hyaenas, <i>Crocuta crocuta</i>	Adults (F, lactating)	Passive ^f	Holekamp et al. (2000)
Giant river otters, <i>Pteronura brasiliensis</i>	Adults (F)	Acoustic (vocalize)	Duplaix (1980)
Banded mongooses, <i>Mungos mungo</i>	Adults (F, lactating)	Acoustic (vocalize)	Furrer, Kunc, and Manser (2012)
White-nosed coatis, <i>Nasua narica</i>	Non-attribute-based	Acoustic, Tactile and Visual (vocalize, groom and tail-up)	Kaufmann (1962)

(continued on next page)

Table 3 (continued)

Species	Attributes of most leaders ^a	Mechanisms to recruit followers	Sources
Ungulates (<i>N</i> =10 species)			
Sable antelope, <i>Hippotragus niger</i> Leicester sheep, <i>Ovis aries</i>	Adult (F, oldest) Non-attribute-based	Unknown Visual (move head)	Stine et al. (1982) Ramseyer, Boissy, Dumont, and Thierry (2009); Ramseyer, Boissy, Thierry, and Dumont (2009)
Domestic goats, <i>Capra aegagrus hircus</i>	Adults (F)	Passive	Escós, Alados, and Boza (1993); J. E. Quílez (personal communication, 2 December 2014)
Thornicroft's giraffe, <i>Giraffa camelopardalis thornicrofti</i> Musk ox, <i>Ovibos moschatus</i>	Adult (F, oldest) Adults (F)	Passive Females=Passive; Males=Coercion	F. B. Bercovitch (personal communication, 24 November 2014); Bery and Bercovitch (2014) Ihl and Bowyer (2011)
Plain zebras, <i>Equus quagga</i> (formerly, <i>E. burchellii</i>)	Adults (F, lactating)	Acoustic, Visual and Coercion (pause, snort and aggression) ^g	I. R. Fischhoff and D. I. Rubenstein (personal communication, 30 November 2014); Fischhoff et al. (2007)
Przewalski horses, <i>E. ferus przewalskii</i>	Adult (F)	Visual (orient in direction of travel before movements); Males=Coercion	Berger (1977); Bourjade, Thierry, Maumy, and Petit (2009); Feist and McCullough (1976)
Domesticated cattle, <i>Bos primigenius</i>	Non-attribute-based	Passive	Dumont, Boissy, Achard, Sibbald, and Erhard (2005); Ramseyer, Boissy, Dumont, et al. (2009)
Charolais heifers, <i>B. taurus</i> African buffalo, <i>Syncerus caffer</i>	Non-attribute-based Adults (F)	Passive Visual (orient in direction of travel before movements)	Reinhardt (1982) Prins (1996)
Cetaceans (<i>N</i> =3 species)			
Hawaiian spinner dolphins, <i>Stenella longirostris</i> Bottlenose dolphins, <i>Tursiops truncatus</i>	Adults Adult (M) ^c	Acoustic and Visual (vocalize, leap, spin and swim in zigzags) Acoustic and Visual (vocalize; side flops)	Lammers and Au (2003); Norris and Johnson (1994) Janik and Slater (1998); Lewis, Wartzok, and Heithaus (2011); Lusseau and Conradt (2009)
Killer whales, <i>Orcinus orca</i>	Adults (F, oldest)	Acoustic (vocalize)	Miller (2002); Brent et al. (2015)
Bats (<i>N</i> =1 species)			
Bechstein's bats, <i>Myotis bechsteinii</i>	Adults (F)	Unknown	Kerth, Ebert, and Schmidtke (2006)

^a Sex-biased leadership: F = females, M = males; Non-attribute-based occurs in the absence of a consistent leader or attribute-based leadership.

^b Note that the 'leader' in these studies was reported to make travel decisions regarding direction irrespective of his position in the travel order.

^c Previously denoted by authors as following a pattern of 'personal' leadership.

^d Data based simply on spatial position within a travelling group, deeming the front monkey to be the leader.

^e Captive, free-ranging group comprised only 3 adults (2 males, 1 female), 3 adolescents (2 males, 1 female) and 1 juvenile female.

^f Most common pattern is passive leadership, but movements in the contexts of border patrols, group hunting and approaches to lions rely upon visual, tactile and olfactory information such as social sniffing, group scent marking and greetings (Holekamp et al., 2000; Smith et al., 2011).

^g Although females lead most often, females rarely use coercion. On occasions with male leaders, coercion is common.

not simply explained by unweaned subadults following their mothers. Instead, lactation remained an important predictor even after nursing offspring were removed from the data set. Perhaps lactating females are the most attractive social partners because they are often accompanied by dependent offspring. For example, Henzi and Barrett (2002) found that adult female baboons with infants are the most attractive social partners. Alternatively, lactating female hyaenas might recruit the most followers prior to reunions because they spend the most time close to the communal den or possess the most accurate knowledge about the current location of the communal den. The communal den is a social hub where clan members gather to socialize, and lactating females visit communal dens more often than other clan members because they must nurse their young cubs there (Holekamp, Cooper et al., 1997).

Rank-related Consensus Costs and Localized Leadership

Among spotted hyaenas, all group members rarely, if ever, occur together concurrently, but large subgroups can emerge to form coalitions to fight lions or neighbouring clans (Smith et al., 2008). Although hyaenas use contact calls to keep in touch at long distances (East & Hofer, 1991; Theis, Greene, Benson-Amram, & Holekamp, 2007), it is unlikely that any individual clan member has global information about the spatial positions of all other clan members at any given time. Instead, our data are consistent with the notion that collective movements often emerge from simple rules and localized interactions (Ballerini et al., 2008). Travelling hyaenas likely rely upon localized rules, such as 'follow adult

females that outrank me'. Thus, despite their apparent social complexity, hyaena groups may in fact represent 'self-organized' fission–fusion systems (Camazine et al., 2003). That is, hyaena clans appear to lack any central authority imposing movement decisions. Instead, as in self-organized flocks of birds or crowds of humans (reviewed by Conradt & List, 2009), coordinated movements appear to be based on localized decisions, which in turn produce complex fission–fusion dynamics.

The highest-ranking adult female in each subgroup of hyaenas was most often the leader at reunions. This finding is inconsistent with the idea that leaders are those individuals with the highest energetic demands (e.g. Rands et al., 2003). Instead, high-ranking adults, on average, have the lowest energetic demands in the clan due to their high priority of access to food (Holekamp et al., 1996). Rank-related leadership likely emerges because low-ranking hyaenas are less attractive social partners and possess less social capital to attract followers than do high-ranking hyaenas (Holekamp, Cooper et al., 1997; Smith et al., 2007). High-ranking adults often benefit from the services provided by subordinates such as help hunting and cooperative defence of resources from lions and members of neighbouring clans (Boydston et al., 2001; Holekamp, Smale, Berg, & Cooper, 1997; Kruuk, 1972).

Although high-ranking leaders may gain more from being followed than low-ranking followers gain from following (Conradt & Roper, 2009), this hierarchical organization may increase the overall efficiency of group decisions (e.g. Henrich, 2006; Nagy, Ákos, Biro, & Vicsek, 2010). Because high-ranking adult females are the most cooperative (Smith et al., 2010) and socially connected

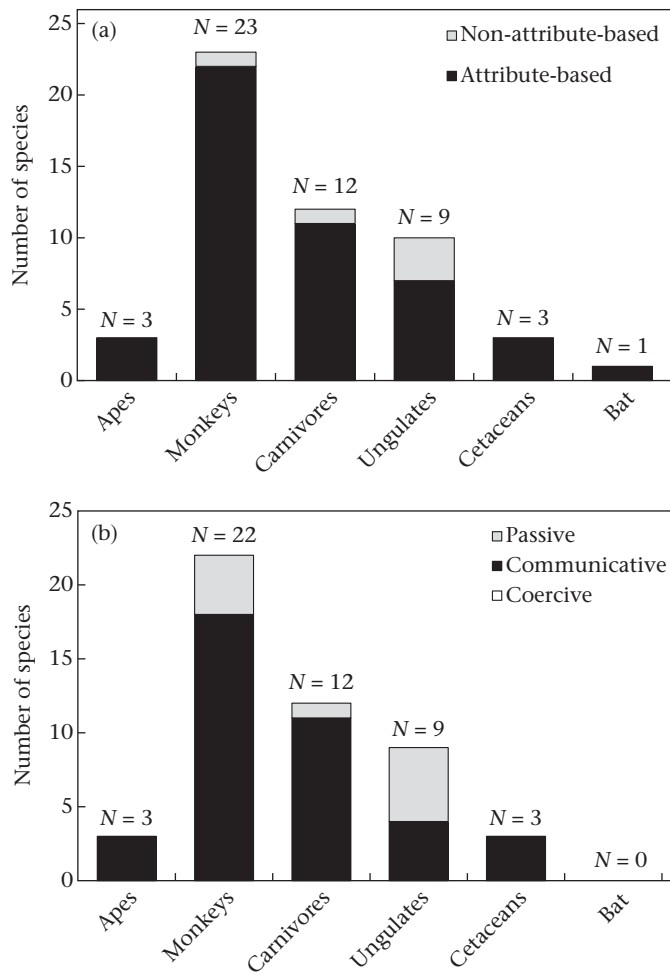


Figure 7. Distribution of mammals best characterized by (a) attribute-based ($N = 48$ species) and non-attribute-based patterns of leadership ($N = 5$ species) and (b) recruitment of followers primarily based on communicative ($N = 39$ species), passive ($N = 10$ species) or coercive ($N = 0$ species) mechanisms. Most primates and ungulates are primarily led by females and primarily rely upon mechanisms other than coercion. However, when male chimpanzees, hamadryas baboons, zebras, horses and musk oxen lead, males use coercion to herd female mates. Mechanisms used by bats are unknown.

clan members (Holekamp et al., 2012), hyaenas might follow the highest-ranking animals within their subgroups to most efficiently integrate with new subgroups at reunions. The short-term costs of following dominants are likely modulated by long-term benefits in the form of increased social and feeding tolerance gained from frequent associations with dominants (Smith et al., 2007).

Given that hyaenas generally associate and cooperate most often with genetic relatives (reviewed by Holekamp et al., 2012; Smith, 2014), as well as those close in rank to themselves (e.g. Smith et al., 2007), travelling subgroups were likely composed of kin and individuals of similar rank. Previous workers have shown that kinship, as well as affiliative and agonistic relationships, influence leader–follower relations in other carnivores (e.g. *Canis lupus familiaris*; Bonanni, Cafazzo, Valsecchi, & Natoli, 2010). Future research should therefore elucidate the extent to which dyadic relationships, such as rank distance, kinship and patterns of cooperation similarly predict leader–follower relations in hyaenas.

Mechanisms of Leadership and Conflict Mitigation at Reunions

Most mammals reviewed here use active recruitment signals to communicate the direction and timing of movements. In contrast,

hyaenas rarely signalled to followers or slowed down when others lagged behind prior to reunions. This finding extends earlier work by Holekamp, Boydston, and Smale (2000), describing hyaenas as relying primarily on passive mechanisms to initiate group travel. There are two possible explanations for our finding that hyaena leaders were more aggressive towards followers in the minutes after than before reunions. First, this might be due to social tolerance rather than coercive facilitation of collective movement. This is consistent with our previous finding that aggression generally promotes subgroup fragmentation rather than cohesion in this species (Smith et al., 2008). Alternatively, because the overall rate of aggression increased during the post-reunion period, this finding may simply reflect increased general agitation among group members after reunions. Regardless, coercion is absent from this context and is surprisingly rare in mammals more generally (e.g. Table 3). On the whole, these findings are consistent with the notion that leadership may evolve in the absence of coercion when leadership resolves coordination problems (Powers & Lehmann, 2014).

Overall, hyaena reunions engender a period of intense arousal manifested as a heightened state of agitation and excitement. Conflict was particularly common at reunions involving food. Just as greetings reduce conflict among humans (Firth, 1972; Kendon & Ferber, 1973) and among spider monkeys, *Ateles geoffroyi* (Aureli & Schaffner, 2007), hyaena greetings reduce fighting among previously separated hyaenas. Our results complement earlier findings showing that conciliatory greetings reduce escalated aggression among hyaenas residing in the same subgroup for extended periods (Colmenares et al., 2000; Wahaj et al., 2001). Although greetings reduce conflict on some occasions, elevated rates of aggression nevertheless generally impose short-term costs on individuals joining new subgroups, particularly in the context of feeding competition. Thus, whereas temporary separations may reduce immediate conflicts of interest, a major contribution of our study is our ability to document that individuals pay consensus costs at subsequent reunions. Further research is now needed to understand the extent to which other species generally suffer from consensus costs at reunions, and whether mechanisms, such as those documented here for the first time in a social carnivore, exist to mitigate conflict at reunions in other species of nonprimate mammals.

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