



Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*

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In animal groups, collective movements emerge from individual interactions. Biologists seek to identify how characteristics of actors in these groups, and their relationships, influence the decision-making process. We distinguished two basic factors determining leadership in group choices: identity and state. We hypothesized that identity is more important to leadership in groups with stable relationships, which permit the development of habitual roles. In groups with fluid membership, particular individuals or subgroups are less likely to emerge as consistent leaders. Instead, we predicted that movement initiation in unstable groups depends on individual state at the time of the decision. We characterized how identity and reproductive state influenced leadership patterns in the movements of plains zebra. As in many other mammals, lactation in this species significantly alters water and energy needs. We investigated leadership in tightly knit harems and loosely bonded herds of multiple harems. Harem females tended to have habitual roles in the initiation of harem movement. In herds, however, we found no consistent leaders among harems. At both levels of social organization, lactation was a key determinant of leadership. In harems, lactating females were more likely to initiate movement than nonlactating females. In turn, harems containing lactating females were more likely to lead herd movements. Thus, we conclude that social relationships and reproductive state together shape the interactions that produce group behaviours. One benefit to lactating females of leading herd movements is preferential access to scarce water. Thus, leadership roles in group decisions may have fitness consequences.

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A central problem in the study of social animals is characterizing the roles of individuals in producing collective behaviours such as group movements (Schaller 1963; Kummer 1968; Prins 1996), cooperative breeding (Covas et al. 2004) or activity synchrony (Côté et al. 1997; Ruckstuhl & Kokko 2002). These group decisions emerge from the interactions of individuals, some of whom may be more central to the outcome (Conradt & Roper 2005). For an individual leading group movement, this role may bring the benefit of greater control over

the timing, distance and direction of the move (Erhart & Overdorff 1999). Groups and societies vary in the extent to which certain individuals are consistent leaders in the initiation of group decisions (Leca et al. 2003). Mountain gorillas, *Gorilla gorilla beringei*, are an example of an animal society in which group decision making is despotic: the dominant male usually leads group movements (Schaller 1963) and females form long-term dominance hierarchies (Robbins et al. 2005). By contrast, in other societies, the identity of the individual initiating a group movement changes over successive movements (Kummer 1968; Erhart & Overdorff 1999; Leca et al. 2003; Overdorff et al. 2005). The initiator of a particular decision may be the one with the strongest need for change at that time (Rands et al. 2003). Individual needs depend on variables

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such as reproductive state, age and health. Thus, we can distinguish between two basic factors determining leadership in the initiation of group choices: identity and state.

We expect identity to have greater weight in group leadership for stable groups, because stability permits habitual leader–follower relationships to develop (Goessmann et al. 2000; Chase et al. 2002; Beacham 2003). Such individually consistent roles in the context of group decisions may emerge independently of whether or not dominance hierarchies exist. By contrast, if group membership changes frequently, we expect that particular individuals or subgroups are less likely to emerge as consistent leaders. Instead, we predict that successful initiation of group choice depends more strongly on needs that can vary over time within an individual.

For wild populations, little is known about how the stability of group associations shapes individual leadership patterns. In one study of ruffed lemurs, *Varecia variegata*, Overdorff et al. (2005) suggested that group stability determines whether certain individuals are consistent leaders of group movement. A stable group of ruffed lemurs contained a dominant female, who led the group more often, but in an unstable group, no individual consistently led movements. To our knowledge, no study has directly tested how group stability shapes leadership roles. We studied leadership in movement within a single species, the plains zebra, which has both stable and unstable social structures. We hypothesized that group stability is a necessary condition for the emergence of consistent individual roles in the initiation of group movement. For unstable groups, we hypothesized that leaders tend to be those whose state prompts them to have the greatest need to move.

Plains zebras are large-bodied grazing equids found in East and southern Africa. Key features of plains zebra sociality and physiology provide the basis for testing our hypotheses. First, plains zebras have a two-tiered social organization (Rubenstein & Hack 2004). The core social group is the harem, consisting of a stallion male, one to several females, and their dependent offspring. Young of both sexes disperse from their natal harem at sexual maturity. Harems are typically stable for months to years. Multiple harems join together to form a herd. Herds are unstable, with associations among harems changing over hours to days (I. R. Fischhoff & D. I. Rubenstein, unpublished data). Second, as females change reproductive state, this modifies their resource needs (National Research Council 1989). The multiple levels of plains zebra social organization, combined with variable female reproductive states, allowed us to characterize the importance of identity and reproductive state for leadership within both the stable harems and fluid herds. For zebras, we can define identity at each level of social organization. Within a harem, the identity of each individual may affect its interactions with other individuals in the harem. Owing to the cohesive nature of harems (Rubenstein 1986), we can assign all individuals in a harem a common harem identity, relative to other harems.

We predicted that the stable relationships within harems would result in individual females taking on consistent positions relative to others in the harem, over

the months to years for which the harem is stable. Furthermore, we expected that lactating females' greater energy and water needs would motivate them to initiate harem movements more frequently than nonlactating females. Thus, we predicted that both individual identity and reproductive state would significantly drive leadership patterns within harems. At the herd level, each harem functions as a cohesive decision-making unit. Owing to the frequent changes in harems composing a herd, we predicted that specific harems would not consistently initiate directed herd movements. However, we expected that the presence of a lactating female in a harem would influence the harem's position in a walking herd. The needs of lactating females cause them to initiate movements of their harem within the herd; therefore, we predicted that 'lactating harems' would be more likely to precipitate herd movements.

To understand the functional significance of initiating movements, we explored how leadership affects resource rewards. For plains zebras, a frequent type of movement is walking to scarce water holes. We expected variation in leadership to have consequences for water access. Within a herd, we expected that lactating harems would reach water earlier than would nonlactating harems. Within a harem, we predicted effects of both lactation and individual identity on arrival order at water holes. Individuals who reach the water hole at the front of the herd may have priority access because there is limited space around a water hole. Arriving earlier at a water hole, we predicted, would correlate with increased likelihood of drinking. Thus, we examined how leadership in movement affected use of a resource critical to survival.

METHODS

Study Population and Field Site

We studied a population of approximately 700 plains zebras in Ol Pejeta Conservancy, a semiarid bushed grassland in the Laikipia ecosystem of central Kenya. Data were collected between July 2003 and August 2005. In our population, we have observed 239 stallions, associated with 396 adult females. Harems vary in size from two to nine adults, including the male (mean \pm SD = 3.5 ± 1.4 individuals, $N = 108$ harems). Eighty per cent of the harems in our study population have three females or fewer. Males and females have different behavioural roles within harems (Rubenstein 1986; Rubenstein & Hack 2004). In the present study, we examined only female–female interactions in leadership within harems.

Herds contain multiple harems and sometimes bachelor groups, which we excluded from the present analysis. In our population, the number of harems in a herd ranged from one to 81 (mean \pm SD = 3.6 ± 5.1 harems, $N = 2544$ herds). Herds making directed movements were significantly smaller (two-tailed Wilcoxon two-sample test: $Z = 7.21$, $P < 0.0001$), ranging in size from one to 18 harems (mean \pm SD = 3.6 ± 2.6 harems, $N = 298$ herds). We analysed harem interactions within herds, treating each harem as a cohesive decision-making unit.

Field Methods

We quantified leadership based on individual position in single-file walking herds, a characteristic formation of zebra groups making directed movements. We considered individuals closest to the front as leaders in initiating a move (Dumont et al. 2005). When we encountered travelling herds, we assigned order for each zebra, relative to the head of the line, which we designated position number one. Although directed movements may continue for up to an hour, we used only one observation for each directed herd movement. For the data collected here, movements typically ended at new grazing locations, water holes or resting sites.

We collected these data by several methods. Every three days, we drove census loops throughout the field site. We also monitored behaviour at water holes and conducted follows of harems. For each herd sighted, we identified the individuals present and classified them into harems. We distinguished individuals based on their unique stripe patterns. In the field, we assigned females to their harem stallions based on typical social interactions such as mutual grooming, male 'herding' of females and mutual responses to movements recorded during behavioural sampling. We determined whether females were lactating by associating foals with their mothers. We made foal–mother assignments based on nursing.

We gathered data on zebra behaviour at water holes through direct observation and remotely, using time-lapse video. As a herd approached within 10 m of a water hole, we recorded the identity of all individuals and the arrival time of each. For every individual, we observed whether it drank during our initial observation of it. Zebras often came close to a water hole but failed to drink during their initial approach; in these cases, they may have returned minutes to hours later.

Analysis

Assumptions about initiation order, travelling position and harem cohesion

We made three assumptions about how an individual's position in groups reflected the process of movement decision making within harems and herds (see Results). Our first assumption was that position in travelling group correlated with the temporal order in which individuals began movement. Second, we assumed that position was stable over the course of a single directed movement. Taken together, these two assumptions justified our use of snapshot observations as an indicator of leadership throughout the move. At the level of the harem, we tested the first two assumptions using our data from focal follows. Based on our field observations, we believe these assumptions to be valid at the level of the herd as well.

Our third assumption was that harem members were highly clumped within herds. Thus, we treated all individuals in a harem as a unit, to which we assigned a position relative to other harems in the herd. We tested this assumption for our data on both travelling herds and herds using water holes. Within travelling herds, we determined the nearest-neighbour distances for each

individual in a harem, measuring distance by relative order. We then computed the Clark–Evans R , which is the ratio of observed mean nearest-neighbour distance (R_o) within the harem to the expected mean nearest-neighbour distance (R_e) if harem members were distributed randomly in the herd (Clark & Evans 1954). We also tested whether individuals within a harem used water holes as a cohesive subgroup within the herd. We used arrival time to order individuals and determined nearest neighbours. For the travelling data, we computed Clarke–Evans R . In this case, we were finding the ratio of observed nearest-neighbour distance in arrival order within harems to the expected nearest-neighbour distance if harem members were distributed randomly within the herd. We also recorded the times elapsed between the arrivals of the first and last individuals in the harem and herd, respectively.

Leadership within harems

We evaluated the effects on leadership of two factors: individual identity and lactation state. We used a mixed model ANOVA, in which lactation state was a fixed effect and individual identity a random effect. We determined the proportion of the variance explained by each factor by computing eta squared (η^2): the ratio of the effect sum of squares over the total sum of squares (Levine & Hullett 2002). At the level of the harem, we included data only for those individuals that we observed at least two times in each state. Harems vary in size, so we normalized observed order relative to harem size. For every female in every sighting, we computed a relative order index between zero and one. Our formula for order index is: $(2 \times \text{position} - 1) / \text{harem size} \times 2$. Scores closer to zero reflect position near the front of the group, in this case the harem. In plains zebras, the male has a qualitatively different role from the females in a harem (Rubenstein 1986). We excluded the stallion male from our analyses. We restricted our analyses to those harems with at least two females.

Leadership in herds

We examined how harem identity and lactation state affected harem position within herds. As we did for the analysis of individuals within harems, we used a mixed model ANOVA, with lactation state as a fixed effect and identity as a random effect. We defined lactating harems as those with at least one lactating female. We included in the ANOVA only harems that we observed at least twice in each state, lactating and nonlactating. We computed order index for each harem in a herd, normalizing for herd size using the same formula applied to females within harems. Thus, in this case, the formula is: $(2 \times \text{position} - 1) / \text{herd size} \times 2$. Here, position refers to harem position and herd size is the number of harems in that herd. We restricted our analysis of herd-level leadership to those herd observations with more than one harem.

Consequences of leadership

We tested whether lactation influenced arrival order at water holes at both harem and herd levels. For harems and herds observed at water, we calculated the same order index used for position in walking groups. In this case, we

ranked them based on their arrival time to the water holes. We used a mixed model ANOVA analogous to that for travelling order analyses.

We hypothesized that individuals arriving earlier had priority access to water holes. To test this hypothesis, we used a logistic regression evaluating the relationship between arrival order among females in a herd and their probability of being observed drinking during their first approach to the water hole. For this analysis, we determined arrival order among all females in the herd. We used absolute order because we predicted that, as group size increased, crowding would reduce an individual's access to space around a water hole.

RESULTS

Assumptions

Initiation order and travelling order

Data collected by following harems supported our assumptions about consistency between initiation order and travelling position, and between travelling position at the beginning and end of directed movements. For 15 harems, we observed initiation order as well as travelling order at the beginning and end of walks. In 292 observations of these harems, all females responded to the initiator. We found a significant linear correlation between initiation order and travelling order (Pearson's correlation coefficient: $r_{290} = 0.88$, $P < 0.0001$). Thus, we can use the position in travelling groups as a measure of the order in which individuals began movement. Furthermore, individuals rarely changed position over the course of a directed movement: individual position in a travelling group at the beginning of moves was strongly correlated with that at the end of movements ($r_{290} = 0.90$, $P < 0.0001$).

Harems' cohesion within herds

To test whether harems segregated within travelling herds, we used a sample of harems that we observed at least 10 times in a herd. Table 1 shows, for each harem, the mean Clark–Evans R , the ratio of observed nearest-neighbour distance to expected distance, averaged over all the sightings of a harem. All means were well below one, indicating that individuals in a harem clumped together within a herd. This result allowed us to assign to each harem a single position relative to other harems within the herd.

Within herds approaching water holes, we found significant clumping in time among individuals within a harem. The mean \pm SD delay between the arrival time of the first and the last member of a harem was 0.7 ± 1.8 min ($N = 192$ harem observations); for herds, the first harem arrived 4.4 ± 7.9 min ($N = 259$ herds) earlier than the last harem (Table 2). These results suggest that all individuals within a harem reached water close to each other in time, relative to individuals in other harems. Taken together, our results from observations of travelling and drinking herds confirm our assumption that harems formed unified subgroups within a herd.

Table 1. Harem cohesiveness within travelling herds

Harem ID number	Number of individuals in harem	Mean travelling $R \pm SE$	Number of observations
01_036	2	0.73 \pm 0.13	14
01_214	3	0.49 \pm 0.14	14
01_270	4	0.63 \pm 0.08	10
01_465	2	0.64 \pm 0.13	13
01_598	3	0.14 \pm 0.07	10
01_793	3	0.72 \pm 0.09	12
01_800	2	0.46 \pm 0.09	15

Cohesiveness of harems within travelling herds, as measured by Clark–Evans R , the ratio of observed mean nearest-neighbour distance (R_o) within the harem to the expected mean nearest-neighbour distance (R_e) if harem members are distributed randomly in the herd (Clark & Evans 1954). For each harem, mean R and its standard error are presented. Mean is averaged over all the sightings of each harem. The mean R for all harems was well below one, indicating that harem members clump together relative to other harems within the herd.

Leadership within Harems

Lactation state and individual identity

We found significant effects on individual position of both lactation (mixed model ANOVA, fixed effect: $F_{1,41.8} = 9.09$, $P = 0.004$, $\eta^2 = 0.02$) and identity ($F_{15,15} = 3.37$, $P = 0.01$, $\eta^2 = 0.09$). The model used travelling observations from 16 females, each from a different harem. For each observation, we computed the female's order index relative to other females in her harem (see Methods). There were 409 order observations for these females, 102 in lactating state and 307 in nonlactating state. Lactating females were closer to the leading edge of travelling harems (Fig. 1). The ANOVA model indicated an estimated difference of 0.12 between the mean order indexes of lactating females (marginal mean = 0.37) and nonlactating females (marginal mean = 0.49).

Leadership in Herds

Lactation state and harem identity

Lactation state had a significant effect on harem position in herds (mixed model ANOVA, fixed effect:

Table 2. Harem cohesiveness within drinking herds

Harem ID number	Number of individuals in harem	Mean drinking $R \pm SE$	Number of observations
2001_214	3	0.17 \pm 0.09	8
2001_307	4	0.57 \pm 0.15	10
2001_403	5	0.73 \pm 0.18	10
2001_565	4	0.65 \pm 0.21	8
2001_596	5	0.48 \pm 0.12	9
2001_725	3	0.14 \pm 0.09	8
2002_1040	5	0.60 \pm 0.15	10

Clumping of harems most frequently observed in herds visiting water holes. Data presented are analogous to those of Table 1. For harems visiting water, the mean R for all harems was well below one, indicating that individuals in a harem clump together within a herd while drinking.

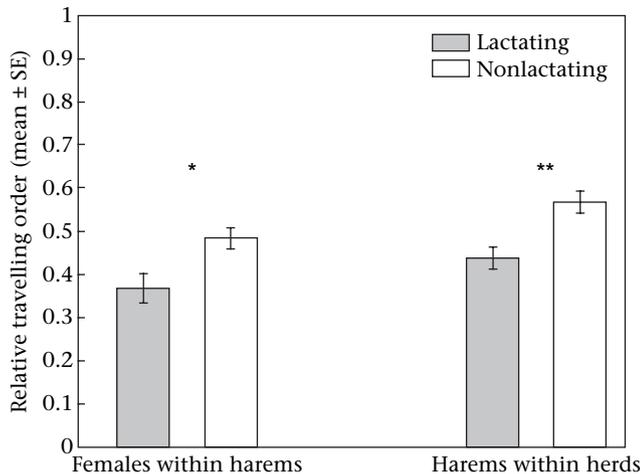


Figure 1. Travelling order index for females in harems and harems within herds. The plot shows the mean order index (marginal mean \pm SE from mixed model ANOVA) for all individuals and harem sightings in either lactating or nonlactating state. Values closer to zero indicate leadership positions. * $P < 0.05$; ** $P < 0.01$.

$F_{1,41.6} = 12.6$, $P = 0.001$, $\eta^2 = 0.04$). However, we found no significant effect of harem identity (mixed model ANOVA, random effect: $F_{28,28} = 1.23$, $P = 0.30$, $\eta^2 = 0.10$). The model used travelling observations from 29 harems. For each observation, we computed the harem's order index relative to other harems in the herd. There were 321 order observations for these harems, 175 in lactating state and 146 in nonlactating state. Harems containing lactating females were closer to the front of herds (Fig. 1). There was an estimated difference of 0.13 between the marginal mean order indexes of lactating and nonlactating harems.

Consequences of Leadership

We examined how lactation and identity influenced the order in which individuals and harems reached water holes. Within harems, we used observations of arrival order to water holes for six females, each in a different harem. For each water hole observation, we computed the female's arrival order index relative to other females in her harem. We observed these individuals 47 times (24 lactating observations, 23 nonlactating observations). At the herd level, we used data from 13 harems. For each water hole observation, we computed the harem's arrival order index relative to other harems in that herd. We observed these harems 95 times (48 observations of harems with at least one lactating female, 47 observations of nonlactating harems).

Within harems, we found no significant effect on water hole arrival order of either individual identity (mixed model ANOVA, random effect: $F_{5,5} = 3.58$, $P = 0.09$, $\eta^2 = 0.13$) or lactation state ($F_{1,6.0} = 2.04$, $P = 0.20$, $\eta^2 = 0.02$; Fig. 2). Within herds, the identity of a harem had no significant effect on its arrival order at water (mixed model ANOVA, random effect: $F_{12,12} = 0.63$, $P = 0.78$, $\eta^2 = 0.07$). However, the presence of a lactating female in a harem resulted in a significantly earlier arrival

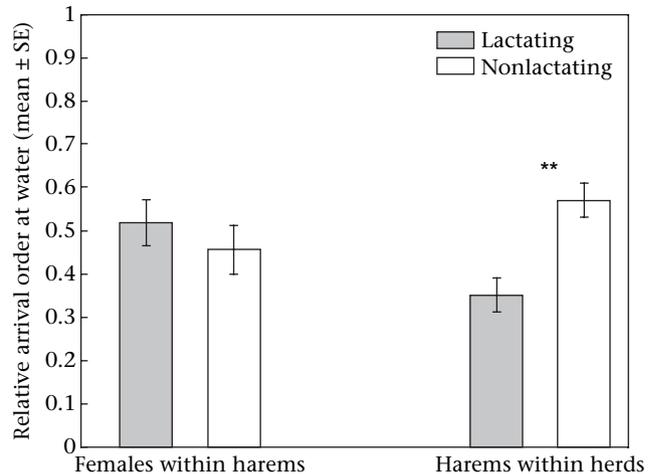


Figure 2. Arrival order to water holes for females within harems and harems in herds. The plot shows the mean order index (marginal mean \pm SE from mixed model ANOVA) for all individuals and harem sightings at water holes in either lactating or nonlactating state. ** $P < 0.01$.

time relative to other harems in the herd ($F_{1,14.1} = 15.42$, $P = 0.002$, $\eta^2 = 0.15$; Fig. 2). By arriving at water close to the front of a herd, individuals in lactating harems were more likely to drink immediately than were individuals that reached water further back within a herd (Wald's test for slope parameter: $t_{13} = 8.15$, $P < 0.0001$; Fig. 3).

DISCUSSION

Understanding the interactions that drive collective decisions is a central goal in biology (Conradt & Roper 2003; Couzin et al. 2005). Behavioural biologists seek to identify how the characteristics of actors and their relationships together influence collective decision-making processes. We expect that those individuals with the greatest motivation to move will most vigorously attempt to initiate

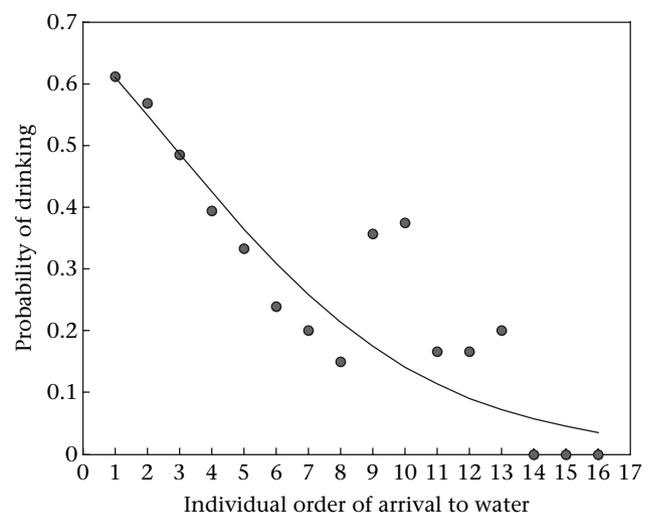


Figure 3. Probability of drinking as a function of an individual's arrival order to water within a herd. The fitted line is a logistic regression. The functional relationship indicates that individuals who are later arrivals within a herd are less likely to be observed drinking.

a group movement. In addition to individual state variables, an individual's influence may depend on the stability of social relationships within the group. In groups where individuals have stable relationships, defined by repeated interactions, there is the potential for despotism: certain individuals may dominate group choice (Schaller 1963; Vehrencamp 1983; Robbins et al. 2005). Where groups are fluid, unstable relationships may prevent individuals from taking on habitual leadership roles. Group decisions in these loose aggregations are likely to be egalitarian, with the most influential individuals for a particular group decision being those with the strongest motivations (Rands et al. 2003). Because individual motivations are driven by state variables that change over time, specific individuals are unlikely to have long-standing roles. Thus, we hypothesize that the stability of social relationships within groups mediates the relative importance of individual identity versus other state variables in defining an individual's leadership potential.

In this study, we characterized how individual identity and needs influenced leadership patterns in the movement decisions of plains zebra. The two-tiered social organization in plains zebras allowed us to investigate leadership in tightly knit harems and loosely bonded herds. As we predicted based on the stability of membership in harems, harem females tended to have consistent positions in the initiation of harem movement. Repeated interactions allowed females to establish habitual roles in the context of movement decisions.

In herds, we found no evidence that harems take on consistent leader or follower positions. We suggest that one reason that decisions are more democratic in a herd is that its harems typically lack the history of interactions necessary to develop habitual leadership roles among themselves. Given the size of herds and the frequency of turnover in harem composition, it is unlikely that all or most of the harems in a given herd have a history of repeated interactions. Future analyses may reveal consistent leader–follower relationships between the pairs or small clusters of harems that more frequently interact.

The fluidity of herds may cause a second mechanism promoting distributed leadership across harems (Leca et al. 2003). Harems in a herd have typically not been moving together for long periods, so we may expect them to have diverse recent experiences. For example, harems may vary in the time elapsed since they last visited water or in the locations that they have recently used for grazing. Thus, harems have varying needs and expectations about which locations will be most rewarding. One apparent consequence is that no harem is consistently among the first or last to move. The diversity of preferences among harems within a herd may explain why travelling herds are typically smaller than herds engaged in other activities. Even when all harems want to move at the same time, they may have different preferred destinations. Therefore, the initiation of herd movement may often result in herd fission.

At both the harem and herd levels, lactation state was a key determinant of individual leadership position. Within the harem, we conclude that lactation results in an individual successfully initiating movement more often, regardless of whether she is a habitual leader. In

turn, the presence of a lactating female in the cohesive harem increases its probability of initiating herd movement. A harem's propensity for leadership fluctuates as its females move between lactating and nonlactating states. By initiating harem movements, lactating females bring their harems to water ahead of other harems. These lactating females and harems benefit from being at the front of herds because they gain priority access to water. Reaching a water hole at the head of a herd significantly increases the probability of drinking in that visit, perhaps because of limited space around the water hole. Access to water in our semiarid study area may be a critical factor for female health and foal survival (Moehlman 2002).

Within harems, we found no significant effect of either state or identity on arrival order at water. Arriving earlier within a harem may be less biologically meaningful than a harem leading a herd. Temporally, all individuals in a harem arrive at water as a cohesive unit, relative to other harems. There was a nonsignificant tendency for identity to affect arrival order, suggesting that dominance may affect access to limited space around a water hole. Similar dominance interactions over water access have been observed in wild horses (Rubenstein 1994).

The stability of relationships influenced the potential for consistent leadership by individuals or harems in our population of plains zebras. In accordance with past models for the emergence of dominance hierarchies (Vehrencamp 1983; Chase et al. 2002), particular individuals or subgroups take on regular leadership roles only if the actors interact repeatedly. In social structures where there is frequent group turnover, state variables influencing needs are stronger predictors of which actors lead decisions. For the most strongly motivated players, initiating movement brings the reward of preferential access to a critical resource.

Our analysis identified lactation and identity as two factors that shape roles in the initiation of movement. However, other factors also contributed to variance in initiation order. For zebras, resource experiences and history of interactions are two additional factors that we expect to influence which individual leads a group movement. As an example of how recent experience affects propensity to lead, we can imagine a lactating female who happens upon a better grass sward than her nonlactating harem neighbours. Although lactating females may generally give up more rapidly on a patch than nonlactating females, in this case we expect a nonlactating female to be the first to move. Over both the short term and the long term, the diversity of movement histories among harems in a herd may result in their having different perceptions of how rewarding the current patch is, relative to other areas they have used. Individuals' history of leader–follower interactions and outcomes is another possible source of variation in leadership. We expect individuals to be more likely to follow others that have previously led them to rewarding locations (Galef 1995). To more fully account for variation in an individual's probability of attempting a lead, and of others responding, we suggest models that include resource experiences and interaction histories.

We have studied leadership patterns in a population with two clearly distinguishable levels of social

organization. In other animal societies, there exists a greater diversity of relationships. Studies of group movement initiation in other populations and species will provide further insight into how group stability shapes the interplay between identity and state as determinants of movement decision making.

For plains zebras and other species, it may be possible to predict how phenotype and social relationships of group members affect the speed, distance or direction of a group move. Recent models show that directed group movements can result from leadership by a small number of goal-oriented individuals (Couzin et al. 2005). Thus, the identity and state of the individuals who first make a move may determine the group movement properties that result. For example, in plains zebra herds, we may expect to find different movement parameters depending on the proportions of lactating and nonlactating individuals in the herd.

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References

- Beacham, J. L. 2003. Models of dominance hierarchy formation: effects of prior experience and intrinsic traits. *Behaviour*, **140**, 1275–1303.
- Chase, I. D., Tovey, C., Spangler-Martin, D. & Manfredonia, M. 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 5744–5749.
- Clark, P. J. & Evans, F. C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, **35**, 445–453.
- Conradt, L. & Roper, T. J. 2003. Group decision-making in animals. *Nature*, **421**, 155–158.
- Conradt, L. & Roper, T. J. 2005. Consensus decision making in animals. *Trends in Ecology & Evolution*, **20**, 449–456.
- Côté, S. D., Schaefer, J. A. & Messier, F. 1997. Time budgets and synchrony of activities in muskoxen: the influence of sex, age, and season. *Canadian Journal of Zoology – Revue Canadienne De Zoologie*, **75**, 1628–1635.
- Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, **433**, 513–516.
- Covas, R., Doutrelant, C. & du Plessis, M. A. 2004. Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. *Proceedings of the Royal Society of London, Series B*, **271**, 827–832.
- Dumont, B., Boissy, A., Achard, C., Sibbald, A. M. & Erhard, H. W. 2005. Consistency of animal order in spontaneous group movements allows the measurement of leadership in a group of grazing heifers. *Applied Animal Behaviour Science*, **95**, 55–66.
- Erhart, E. M. & Overdorff, D. J. 1999. Female coordination of group travel in wild *Propithecus* and *Eulemur*. *International Journal of Primatology*, **20**, 927–940.
- Galef, B. G., Jr. 1995. Why behavior patterns that animals learn socially are locally adaptive. *Animal Behaviour*, **49**, 1325–1334.
- Goessmann, C., Hemelrijk, C. & Huber, R. 2000. The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. *Behavioral Ecology and Sociobiology*, **48**, 418–428.
- Kummer, H. 1968. *Social Organization of Hamadryas Baboons*. Chicago: University of Chicago Press.
- Leca, J. B., Gunst, N., Thierry, B. & Petit, O. 2003. Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Animal Behaviour*, **66**, 1045–1052.
- Levine, T. R. & Hullett, C. R. 2002. Eta squared, partial eta squared, and misreporting of effect size in communication research. *Human Communication Research*, **28**, 612–625.
- Moehlman, P. D. 2002. *Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan*. Gland, Switzerland: IUCN.
- National Research Council 1989. *Nutrient Requirements of Horses*. Washington, D.C.: National Academy Press.
- Overdorff, D. J., Erhart, E. M. & Mutschler, T. 2005. Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? *American Journal of Primatology*, **66**, 7–22.
- Prins, H. H. T. 1996. *Ecology and Behaviour of the African Buffalo: Social Inequality and Decision Making*. London: Chapman & Hall.
- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M. & Johnstone, R. A. 2003. Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, **423**, 432–434.
- Robbins, M. M., Robbins, A. M., Gerald-Steklis, N. & Steklis, H. D. 2005. Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank. *Behaviour*, **142**, 779–809.
- Rubenstein, D. I. 1986. Ecology and sociality in horses and zebras. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), Princeton, New Jersey: Princeton University Press.
- Rubenstein, D. I. 1994. The ecology of female social behavior in horses, zebras, and asses. In: *Animal Societies: Individuals, Interactions, and Organization* (Ed. by P. Jarman & A. Rossiter), pp. 13–28. Kyoto: Kyoto University Press.
- Rubenstein, D. I. & Hack, M. 2004. Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In: *Sexual Selection in Primates: New and Comparative Perspectives* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 266–279. Cambridge: Cambridge University Press.
- Ruckstuhl, K. E. & Kokko, H. 2002. Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Animal Behaviour*, **64**, 909–914.
- Schaller, G. 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press.
- Vehrencamp, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, **31**, 667–682.