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Leadership in mixed-sex groups of muskoxen during the snow-free season

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In social ungulates particular individuals or cohorts, such as adult females, can lead or initiate foraging movements. We use muskoxen (*Ovibos moschatus*) as a model system to test hypotheses regarding the sex and age class of leaders and the potential costs of leadership in 3 different behavioral contexts: activity initiation, foraging-bout movements, and spontaneous group movements. We conducted research on approximately 160 muskoxen at Cape Krusenstern National Monument adjacent to the coast of the Chuckchi Sea in northwestern Alaska. We observed free-ranging, mixed-sex groups of muskoxen from the ground during 5 June–22 September 2002. Adult females emerged as leaders in all 3 contexts, and other group members were more likely to follow adult females than adult males during initiations of activity. Half of successful initiations by adult males included aggressive behavior toward females. Males took a more active role during rut (the mating season) by provoking females to initiate group activity and by actively manipulating spontaneous movements led by females through herding and blocking activities. Leaders incurred no obvious costs in terms of lost foraging time. Costs and benefits of leadership can be subtle and difficult to measure in the field and can include foraging and reproductive trade-offs and increased risk of predation.

Key words: behavior, foraging, groups, leadership, movements, muskoxen, *Ovibos moschatus*, sociality

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To maintain group cohesion group-living animals in search of resources must reach a collective agreement on where to go. How they accomplish that coordination is an area of increased interest among biologists (King et al. 2009). Such collective-group decisions can be achieved in different ways. Couzin et al. (2005) modeled how movements of large groups are possible without direct leadership, as long as only a few informed individuals are present and all group members adhere to a few simple rules of movement. Such leadership by numbers (Couzin et al. 2005) might be the only group decision-making process available to very large aggregations such as migrating wildebeest (*Connochaetes taurinus*) or fish shoals, where each group member can communicate only with its nearest neighbors. In small foraging groups of ungulates, however, where all members can communicate with each other, leadership and decision-making behaviors can be more complex and determined by social interactions (Conradt and Roper 2005, 2009; King and Cowlishaw 2009; Ramseyer et al. 2009a). In smaller groups individual animals (Dumont et al. 2005) or members of a particular sex–age group can serve as leaders of group movements (Reale and Festa-Bianchet 2003) or initiators of group activity (Leca et al. 2003). Prins (1996) observed what he termed voting among female African buffalo (*Syncerus caffer*)—animals stood up during resting bouts and positioned their bodies in a preferred direction of travel. Increases in activity also can precede such movements (Ramseyer et al. 2009a, 2009b). Collective group decisions might not be equally advantageous for all group members because of differences in nutritional needs or reproductive status, and leaders themselves can pay a cost through lost foraging time or increased exposure to predators (Conradt et al. 2009; Conradt and Roper 2003, 2009; Sumpter 2009).

Studies of group leadership in social animals often are placed into 3 broad categories: theoretical models of potential mechanisms of group movements (Ame et al. 2006; Couzin et al. 2005) or costs and benefits to leaders and followers (Conradt and Roper 2003, 2009); experimental studies involving captive or domestic animals (Lachlan et al. 1998;

Levin 1996; Ramseyer et al. 2009a, 2009b; Reebs 2000); and, rarest of all, empirical observations from free-ranging populations (Boinski 1993; King and Cowlishaw 2009; Lusseau and Conradt 2009; McComb et al. 2001; Petit et al. 2009), some of which are anecdotal (Miller et al. 1972).

A challenge for those studying group leadership is determining how leaders can be identified in the field. Leadership can depend on season or behavioral context. For example, in ungulates, leaders can emerge during spontaneous long-distance group movements but not during slow daily foraging movements (Dumont et al. 2005). A leader traditionally is considered to be the animal in the front of a group movement (Kiflawi and Mazeroll 2006; Miller et al. 1972). Although animals in the front position can direct group movements (Bumann and Krause 1993; Reebs 2000), positioning of leaders might be difficult to distinguish in slow foraging-bout movements (Dumont et al. 2005) and in small groups where all members can communicate with each other by visual, olfactory, or auditory signals (Boinski 1993; King and Cowlishaw 2009).

Muskoxen (*Ovibos moschatus*) typically live in groups of 10–40 animals in an environment that exhibits strong seasonality (Gray 1987; Heard 1992). Muskox groups tend to be nonmigratory (Gray 1987). In the Arctic forage quality and quantity (Klein 1990; Klein and Bay 1990) and nutritional needs of large herbivores (White 1983) undergo large seasonal changes (Crater et al. 2007). Under these conditions, animals can enhance their fitness by making fine-scale decisions on where and when to feed (White 1983). Groups would benefit from the knowledge and memory of their most experienced individuals to maximize their seasonal foraging success. Knowledge of the sex and age class of such group leaders, and their role during group movements, also is important for conservation of muskox populations, especially when hunting quotas on different sex–age classes are set. In mixed-sex groups of foraging ungulates adult females are the most likely to lead (Gray 1987; Prins 1996), because they are followed by their young (Rowell 1991), or because they have the greatest nutritional need (Barboza and Bowyer 2000, 2001) and therefore are motivated (sensu White 1983) to lead foraging movements.

Motivations for group formation and movements can be nutritional, physiological, related to avoidance of predators, sociality, or be motivated by a combination of these factors. Nevertheless, group movements by muskoxen can differ in characteristics such as speed, distance traveled, and activities of individuals during movements. We identified the sex and age class of leaders in groups of muskoxen in 3 different behavioral contexts: initiators of group activity after resting bouts (Boinski 1993; Leca et al. 2003); leaders (occupying the front position) of slow foraging-bout movements (Dumont et al. 2005); and leaders of apparently spontaneous group movements (Dumont et al. 2005). These spontaneous movements are relatively fast and cover longer distances than those associated with foraging bouts. We tested the hypothesis that leaders would emerge during initiations of activity and spontaneous group movements but not during slow foraging-bout movements, when subtle communication between group members would be more likely than in larger, faster-moving groups. We further hypothesized that adult females would be more likely to lead and are more likely to be followed than males, and that leaders would incur a cost through reduced time spent feeding.

Materials and Methods

Study area.—Cape Krusenstern National Monument is 2,670 km^2 adjacent to the coast of the Chuckchi Sea in northwestern Alaska (Ihl 2010). Vegetation throughout the monument is arctic coastal tundra. Beach ridges and extensive lagoons characterize areas near the coast, and several clusters of hills $\leq$ 613 m in elevation occur further inland and are used as wintering areas by muskoxen. Hilltops are generally barren and windswept, with *Dryas* heath and hummocky tundra dominating as contiguous bands along hill slopes. These clusters of hills are separated by wide expanses of gently rolling tussock tundra. Winters are long and cold with frequent severe windstorms; summers are cool with most precipitation occurring in August. Average minimum temperature was -24.4°C in February, and average maximum temperature was 15.1°C in July (Ihl 2010). Gray wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) are the primary predators of muskoxen.

After extirpation from Alaska in the late 1800s (Lent 1999), muskoxen were reestablished to northwestern Alaska in recent decades (Coady and Hinman 1984). In 1970 and 1977, 36 and 34 muskoxen, respectively, were released near Cape Thompson in northwestern Alaska. After growing slowly for 2 decades the population began to increase steadily in the early 1990s (Dau 2005). The population subsequently increased and spread south to occupy Cape Krusenstern National Monument with current estimates of approximately 350–400 animals (Ihl 2010). An aerial survey conducted in April 2002 counted 163 muskoxen living in Cape Krusenstern National Monument (B. Shults, Western Arctic National Parklands, United States National Park Service, pers. comm.).

Sampling procedures.—All sampling procedures conformed to the guidelines for use of mammals in research approved by the American Society of Mammalogists (Gannon et al. 2007). We followed free-ranging, mixed-sex groups of muskoxen on foot during 5 June–22 September 2002. Data collection encompassed 2 periods: summer (11 June–9 July 2002) and rut (15 July–22 September 2002). Although mating (rutting) generally does not commence until mid-August, we observed intense courtship and competitive behaviors by adult males as early as 15 July. Thereafter, we did not observe $>$1 adult male per group. Consequently, we grouped data from the 2nd one-half of July with the rutting period. We selected these 2 intervals for sampling because they represent periods during which changing group size and social behavior (Gray 1987; Heard 1992) might affect leadership in muskoxen.

We defined a group as any number of animals within 50 m of their nearest neighbors that maintained cohesiveness while

moving and traveling together in the same direction. If a question arose as to whether an animal was part of a group, we watched that animal until it joined the group or moved away. Repeated observations of the same animals were unavoidable because the study population numbered only ~160 animals. During summer and rut muskox groups were transient and repeatedly broke apart and reformed into new groups (Ihl 2007). We considered newly formed groups as unique observations, even if they contained some of the same individuals we observed previously.

During summer we collected data during 2 field trips: 11–21 June and 5–9 July. We sampled the rutting period in 4 field trips, 15 July–23 July, 5–13 August, 24 August–3 September, and 16–22 September. We initially located muskox groups from fixed-wing airplanes at the beginning of each sampling period. We then selected a location for our base camp and from there approached muskox herds on foot. We observed animals through a 20–60× spotting scope and 8 × 40 binoculars from distances of 100–1,500 m. We observed each group as long as visibility, weather, daylight, and observer stamina allowed. During June and July observations took place throughout the diel cycle but with most observations focused between 1000 and 0000 h. At all other times we restricted observations to daylight hours.

We determined age and sex of muskoxen on the basis of horn development, body size, and coat length. We categorized muskoxen as young, yearlings, adult females (≥2 years old), 2-year-old males, and adult males (Gray 1987). We placed 2-year-old males in a separate category; although not reproductive, these males remained within mixed-sex herds even during rut, indicating that their status in the group differed from that of solitary adult males. We observed 2-year-old females nurse young on several occasions and therefore grouped them with adult females.

Initiators of activity were animals that rose 1st, left the resting area of the group, and began a new activity after a resting bout. A successful initiation was defined as >80% of herd members following the initiator by also rising and joining in the activity. For each initiation we recorded the time elapsed until 80% of the herd had followed the initiator. Leaders of foraging-bout movements were the animals occupying the front position when >80% of the herd was moving slowly in the same direction while foraging. Spontaneous group movements differed from foraging-bout movements in that animals were either running or walking the entire time that we made observations; these animals did not forage and typically traveled >100 m in 1 min. Leaders of spontaneous group movements were the animals initiating the movement and occupying the front position. Spontaneous group movements were typically much faster and covered more distance than foraging-bout movements. For each spontaneous group movement we recorded the destination of the group (e.g., feeding or resting areas) and the activity immediately following that movement. We also noted whether the group split or whether the group was blocked or interrupted by the adult male. We scanned groups at 15-min intervals (Altmann 1974) to describe behavior of all group members. During those scans we recorded the sex and age class of each individual and whether each animal was feeding, walking, standing, lying, or engaging in sexual or aggressive interactions (Gray 1987).

Data treatment and statistical analyses.—We acknowledge that we sampled individuals more than once during our study. Because our sampling unit was the group, and the goal of our study was to characterize behavior of individuals within a particular group context, no other sampling methodology was possible, especially in this remote arctic setting. Most individuals could not be recognized individually, and this could have led to some bias in our analyses because of pseudoreplication.

We used the *G*-statistic (Sokal and Rohlf 1969) to test ($\alpha = 0.05$) the observed distribution of leaders in all 3 contexts against a null model assuming equal distribution of leadership among all sex–age classes. We tested whether leadership by any sex–age class differed significantly from the proportion of that sex–age class in the population. Similarly, in a small group with 7 known individuals we used the *G*-statistic to test whether leadership was distributed equally among individuals. We used the 2-tailed *t*-test for unequal variances ($\alpha = 0.05$) to compare lag times until the group followed male and female initiators of activity. We used 2-sample *t*-tests for unequal variances to test for seasonal differences in group size and seasonal differences of percentage of males in groups. Because our sample sizes are small, which limits utility of tests for skew and kurtosis, we inspected our data visually and found that distributions were approximately normal. We also used the *G*-test with Yates' correction (Sokal and Rohlf 1969) to test for differential success between males and females when initiating activity bouts. The *G*-test was used to examine potential costs of leadership by comparing active time spent feeding (i.e., foraging efficiency—Berger 1978) versus not feeding between leaders and nonleaders. We used Systat 10.2 (Systat Software, Inc., Chicago, Illinois) for all analyses except *G*-tests, which we performed manually according to Sokal and Rohlf (1969).

Results

Population demographics and group composition.—The study population contained 3% adult males, 56% adult females, 13% 2-year-old males, and 29% yearlings and young during summer 2002. Mean (± *SE*) group size was 19.00 ± 2.21 muskoxen. During rut 2002, 14% of individuals were adult males, 40% adult females, 18% 2-year-old males, and 28% yearlings and young. Mean (± *SE*) group size was 10.8 ± 0.9 muskoxen. Summer groups were significantly larger than rutting groups ($t_{31} = 3.44$, $P < 0.0017$) and contained a smaller percentage of adult males ($t_{29} = -6.81$, $P < 0.0000$).

During summer we observed 24 mixed-sex groups during 13 continuous observation periods lasting from 15 to 525 min. Observations of groups are sometimes larger than continuous observations, because during some periods we could observe

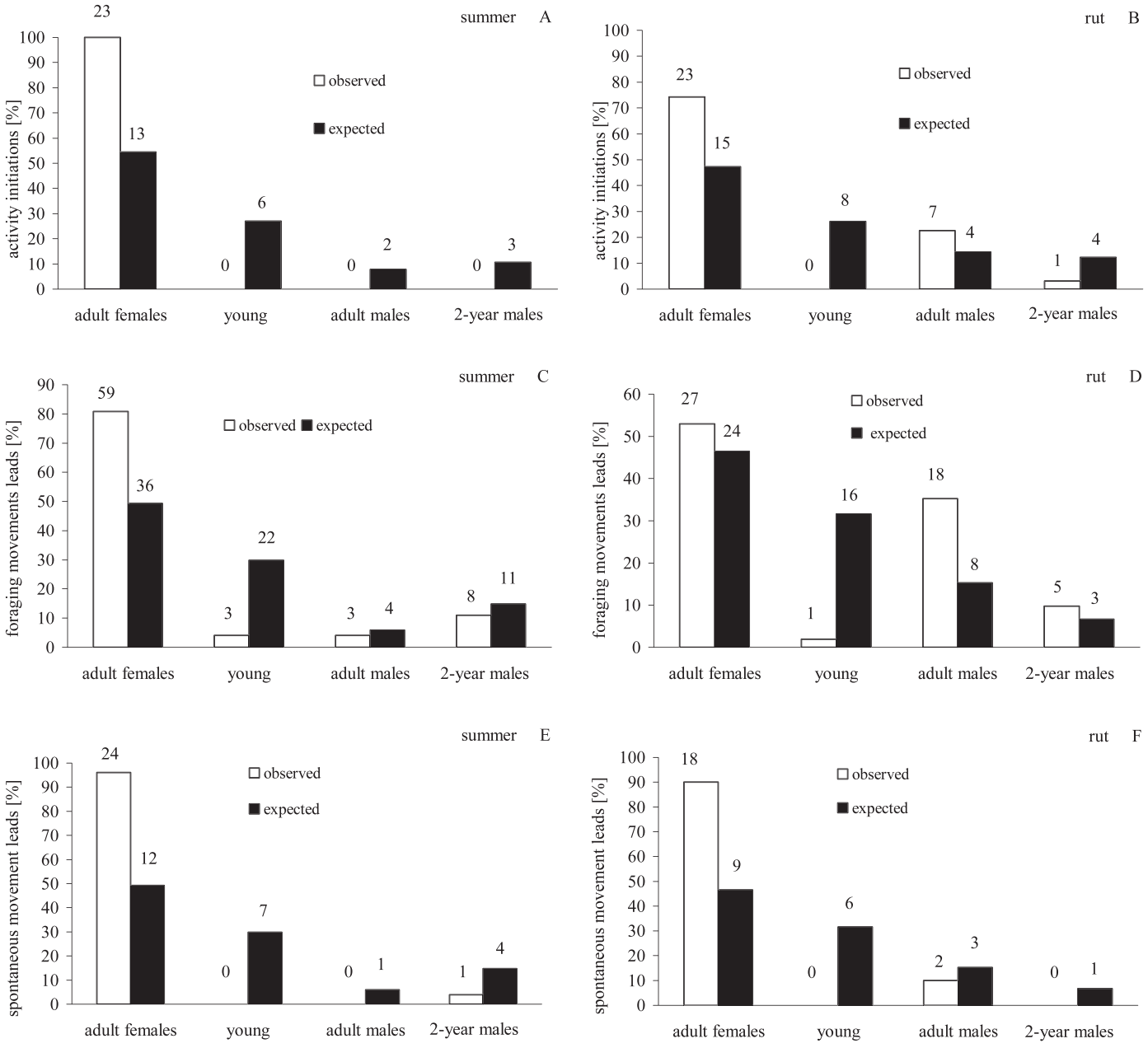

FIG. 1.—Group leadership in muskoxen in 3 behavioral contexts—activity initiations (top row), foraging-bout movements (middle row), and spontaneous group movements (bottom row)—in summer and rut at Cape Krusenstern National Monument, Alaska, June–September 2002. Sample size (n) is above each bar.

>1 group simultaneously. During rut we observed 14 mixed-sex groups during 21 continuous observation periods lasting from 75 to 660 min.

We recorded 67 attempts to initiate group activity after resting bouts by group leaders. Of these, 54 ($n = 23$ during spring–summer and $n = 31$ during rut) were successful. Foraging-bout movements composed 29% ($n = 73$ during spring–summer and $n = 51$ during rut) of group scans collected during activity bouts. We observed 45 spontaneous group movements ($n = 25$ during spring–summer and $n = 20$ during rut).

Initiators of group activity.—Adult female muskoxen were initiators of group activity (Figs. 1A and 1B) during summer ($G_3 = 22.64$, $P < 0.001$) and rut ($G_3 = 21.64$, $P < 0.001$). Although adult males appear to initiate more activity bouts than expected, our sample size was too small to test this statistically (Fig. 1B). Females were more likely to be followed by group members than were males ($G_1 = 3.95$, $P < 0.05$; Table 1). The mean ($\pm$ *SE*) lag time until >80% of the group followed a male (16.59 $\pm$ 1.99 min) or female (20.13 $\pm$ 4.03 min) did not differ ($t_{11} = -0.79$, $P = 0.45$). Although females always initiated activity bouts by beginning

Table 1.—Successful and unsuccessful initiations of group activity by male and female muskoxen, and behavior of activity initiators in mixed-sex groups of muskoxen, at Cape Krusenstern National Monument, Alaska, June–September 2002.

	Activity initiators			
	Females		Males	
	n	%	*n*	%
Total activity initiations[a]				
Successful attempts[b]	46	86.8	8	57.1
Unsuccessful attempts	7	13.2	6	42.9
Success of initiation behaviors by leaders				
Foraging				
Unsuccessful attempts	7	13.2	4	28.6
Successful attempts	46	86.8	4	28.6
Aggression toward males				
Unsuccessful attempts	0	0	1	7.1
Successful attempts	0	0	0	0
Aggression toward females				
Unsuccessful attempts	0	0	1	7.1
Successful attempts	0	0	4	28.6

[a] Differs between males and females ($G_1 = 3.95$, $P < 0.05$).
[b] Activity initiation was successful if ≥80% of the group followed the initiator.

to forage, 43% of initiations by males involved aggression toward other group members (Table 1). Males succeeded more often in initiating activity if they were aggressive toward females (4 of 5 attempts) than if they began foraging (4 of 8 attempts; Table 1).

Leaders of foraging-bout movements.—Leadership of foraging-bout movements differed from a random pattern in summer ($G_3 = 39.32$, $P < 0.0001$) and during rut ($G_3 = 35.52$, $P < 0.0001$). During summer adult females led most foraging-bout movements, and observed leadership by females was >30% higher than expected values (Fig. 1C). During rut adult males leading foraging-bout movements exceeded expected values by >50% (Fig. 1D). Adult females led more movements overall, but numbers were not greater than expected (Figs. 1C and 1D).

Leaders of spontaneous group movements.—Adult females dominated as leaders of spontaneous group movements (Figs. 1E and 1F) in both summer ($G_3 = 25.56$, $P < 0.0001$) and during rut ($G_3 = 18.60$, $P < 0.0001$). Only 1 spontaneous group movement in summer and 2 during rut were led by males (Figs. 1E and 1F). During summer 36% of spontaneous group movements led to a new feeding area, 16% led to an area where the group rested, 24% resulted in the joining of another group, and 24% were unsuccessful in that <80% of the group followed, thereby resulting in a splitting of the group (Table 2). During rut 50% of spontaneous movements were blocked or interrupted by the dominant male in the group (Table 2; Fig. 2), and only 30%, 10%, and 10% led to feeding and resting areas or the splitting of the group, respectively (Table 2).

Leadership by individuals, and costs of leading.—In a small group with 7 known individuals (1 adult male, 3 adult females, one 2-year-old female, and 2 young) that we observed during rut, leadership among all adult members did not differ from a random pattern during 13 activity initiations ($G_4 = 0.48$, $P = 0.98$) and 12 spontaneous group movements ($G_4 = 3.94$, $P = 0.41$; Fig. 2). Nonetheless, during 23 foraging-bout movements the adult male led more often than expected ($G_4 = 16.49$, $P = 0.002$) from a random pattern (Fig. 2). The adult male took advantage of topographic features such as coast lines, willow (*Salix* sp.) thickets, or rock outcroppings when attempting to block and manipulate female movements, and typically continued that harassment until females abandoned their attempt to move in their initial direction.

Table 2.—Outcome of spontaneous group movements by mixed-sex groups of muskoxen at Cape Krusenstern National Monument, Alaska, June–September 2002.

Destination or outcome of spontaneous group movements	Season			
	Summer		Rut	
	n	%	*n*	%
Move to new feeding area	9	36	6	30
Move to resting area	4	16	2	10
Group joins another group	6	24	0	0
Group splits	6	24	2	10
Movement interrupted by adult male	0	0	10	50

Initiators of group activity and leaders of foraging-bout movements of either sex did not spend less time feeding than nonleaders of the same sex (Fig. 3). This outcome indicates that leaders did not incur a substantial cost in terms of lost feeding time after initiating activity bouts (females: $G_1 = 0.58$, $P = 0.45$; males: $G_1 = 2.13$, $P = 0.14$) or while leading foraging-bout movements (females: $G_1 = 0.88$, $P = 0.35$; males: $G_1 = 0.1.10$, $P = 0.29$).

Discussion

Group decision-making by muskoxen is not a random process; adult females typically lead more often than other sex and age classes, especially during summer, an outcome observed in taxa as diverse as fish (Kiflawi and Mazeroll 2006), primates (Boinski 1993; Leca et al. 2003), and other ungulates (Dumont et al. 2005; Prins 1996). Leadership differed from random patterns in all 3 behavioral contexts we studied. These results support our hypotheses that leadership would emerge during activity initiation and spontaneous group movements but is contrary to our hypothesis that the lead position during foraging-bout movements would be occupied randomly. Leadership of groups was most pronounced during spontaneous group movements in both summer and rut. These movements, more so than foraging-bout movements or activity initiation, had the potential to change the situation of the entire group, because such movements led to new feeding areas, resting areas, or resulted in the fission or fusion of muskox groups.

Leadership patterns in muskoxen underwent seasonal changes. During rut adult males took a more active role in all 3 movement types we studied. Rutting males initiated

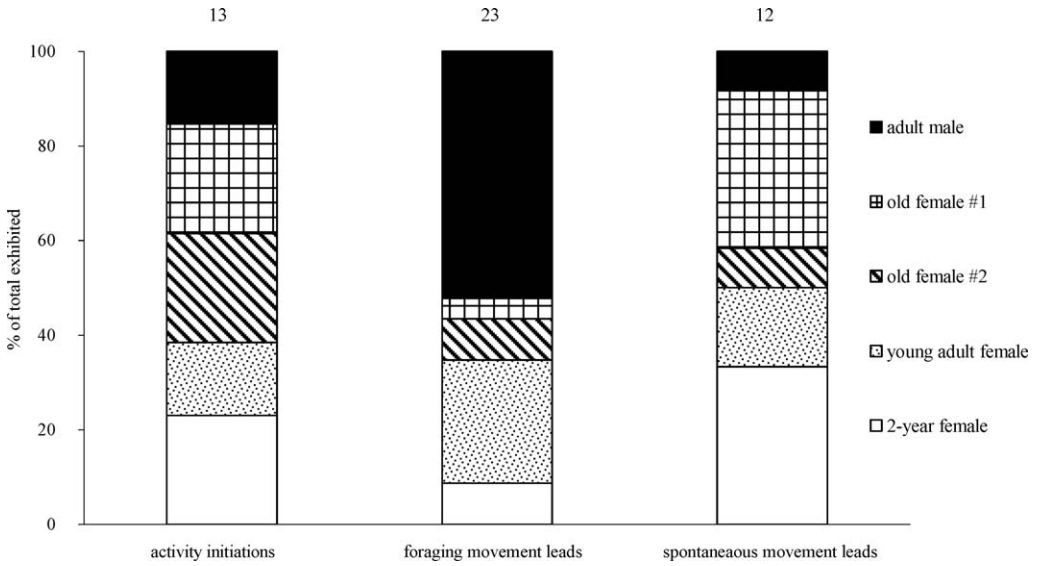

Fig. 2.—Distribution of leadership during activity initiations, foraging-bout movements, and spontaneous group movements among the 5 adult members of a free-ranging muskox group during rut at Cape Krusenstern National Monument, Alaska, June–September 2002. Sample size (*n*) is above each bar.

changes in group activity 43% of the time by provoking females to commence courtship or by chasing females or other males. Males were not involved, however, in spontaneous group movements as in other behavioral categories during rut.

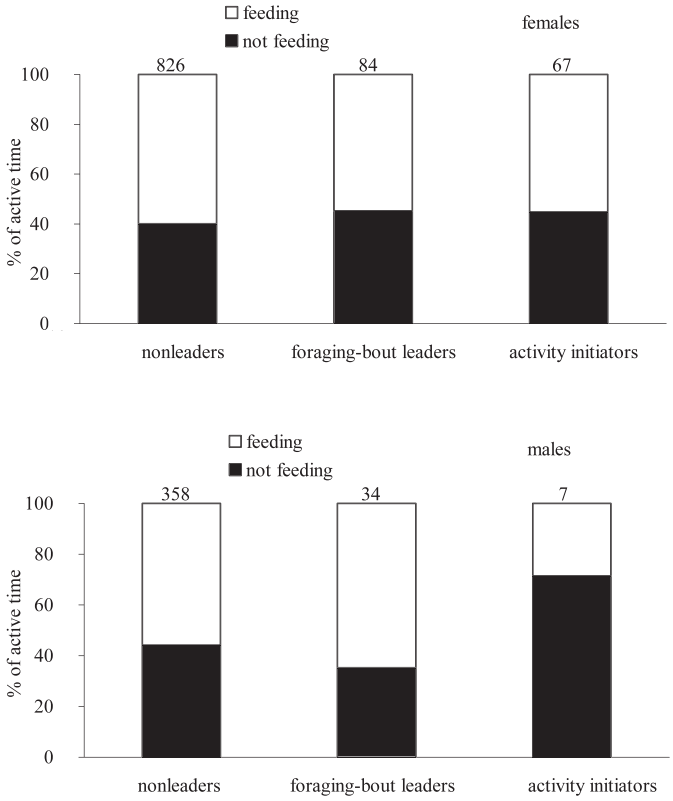

Fig. 3.—Leadership costs in terms of active time spent feeding by nonleaders and leaders of activity initiations and foraging-bout movements in muskoxen at Cape Krusenstern National Monument, Alaska, June–September 2002. Sample size (*n*) is above each bar.

Nevertheless, males were particularly active in interrupting attempts at spontaneous group movements initiated by females during rut. During foraging movements, following such repeated interruptions, females often followed the male. Because of the sometimes large distances at which we made observations, we cannot be sure that males did not use a subtle communication to initiate spontaneous movements. We did not perceive such signals, however, when we made observations at closer distances. Another possibility is that a male stopping a spontaneous movement simply caused another spontaneous event by females. In areas of high muskox densities male–male competition for females during rut also might lead to fission of groups (Gunn 1992).

Although limited, examination of data on the role of individuals in leadership indicated that the leadership role is not dominated by 1 individual but tends to be shared by all adult females in the group during initiation of activity and spontaneous group movements. Nontheless, in our small group with known individuals, the adult male led 52% of all foraging movements during rut. Female ungulates seek out groups with large males during rut (Bowyer et al. 2007); evidence is increasing that such males synchronize estrus (Rowell et al. 2007; Whittle et al. 2000). How such changes in group size, composition, and social behavior might influence leadership, however, remains largely unstudied. In contrast, Dumont et al. (2005) observed the same individual in a group of 15 domestic heifers lead 48% of spontaneous group movements but reported no such leadership during foraging-bout movements. Rowell (1991) observed that flocks of domestic sheep were led by the oldest female in 82% of observations. We could not identify individual animals consistently, and the same muskoxen undoubtedly were observed repeatedly in groups with different compositions of individuals. Consequently, we might have increased the probability of making a type I error by some unknown amount.

Theoretical models of group leadership (Ame et al. 2006; Conradt and Roper 2003, 2005; Couzin et al. 2005) rely on estimating the potential costs and benefits to leaders and followers. Conradt and Roper (2003, 2005, 2009) hypothesized that leaders should be the individuals with the highest consensus costs, for which following would be more costly than leading, whereas followers should be those group members for which following was less costly than either leading or making solitary movements. Nevertheless, we detected no significant difference in time spent feeding among leaders versus nonleaders of either sex in muskox groups. Perhaps leadership costs are subtle and must be measured at a much finer scale of foraging or in a different currency, such as predation risk (Bumann et al. 1997). Gray wolves are most successful in hunting muskoxen if they succeed in enticing the group to give up their defensive formation and run; animals in the rear of the group can be the most vulnerable (Mech 1988). Costs of leadership are difficult to quantify among free-ranging animals, and resolution of this question might be better addressed by an experimental approach with captive animals and using settings in which predation risk can be simulated.

A remaining question in studies of group leadership is how the transfer of information from leaders to followers occurs and how group members determine which individuals to follow (Conradt and Roper 2005; Reebs 2000). In some animal societies leaders use specialized signals to relate information, such as the location of food sources, to group members (von Frisch 1967). Nonetheless, leadership is possible without a transfer of information to followers (Couzin et al. 2005). Adult female muskoxen simply might move 1st because they are the most experienced and therefore most confident group members or have the greatest physiological drive to forage. Strong cohesion among female group members might be further enhanced in social ungulates with prolonged mother–daughter associations, where small groups can consist of female kin and older females, in which mothers have automatic followers in their daughters (Green et al. 1989; McComb et al. 2001; Rowell 1991). Young females can learn from their mothers how to be future leaders (Klein 1999). This female–young association could explain why groups followed female initiators of group activity more often than male initiators.

In contrast to females, males lead by actively manipulating the movements of other group members during rut. The main motivation of males during rut is not foraging but to keep estrous females under their direct control and prevent access of competing males to females (Gray 1987). The social behavior of adult males during rut, however, still might result in them becoming leaders. A possible cost of increasing social interactions with females and other males is a loss of feeding time for initiators of activity. Due to larger group sizes in summer, the percentage of adult males in muskox groups during summer was lower than during rut, and males had a limited role in group leadership during that time. Because of their larger body size, adult male ungulates have different nutritional needs than females (Barboza and Bowyer 2000, 2001) and might be less vulnerable to predation as long as they remain within groups. Outside of rut males might incur less cost to move alone or in small bachelor groups than to follow groups of females. Adult males that stay with female groups outside rut typically exhibit less synchrony with the group than do females (Côté et al. 1997).

Females predominated as leaders of spontaneous group movements and were influential in determining which feeding and resting areas groups of muskoxen used. Female leadership also influenced group sizes because in some instances it resulted in the fission or fusion of groups. Males, however, interfered with female leadership by actively blocking or manipulating group movements during rut. Leadership costs are likely subtle and vary depending on the nutritional, physiological, and hormonal status of individuals. Costs of following should be lowest among members of the same sex and age group, because they share similar nutritional needs and foraging strategies (Barboza and Bowyer 2000, 2001). Costs might have to be measured in a different currency than time spent feeding. Our study provides the 1st empirical study of group leadership in free-ranging muskoxen. We documented that adult females are the most active leaders in a variety of group movements, as is typical of other ungulates, but that leadership context changes seasonally under the influence of rutting males.

Acknowledgments

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