Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*

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Abstract: We analyzed the leadership behavior of breeding and nonbreeding gray wolves (*Canis lupus*) in three packs during winter in 1997–1999. Scent-marking, frontal leadership (time and frequency in the lead while traveling), initiation of activity, and nonfrontal leadership were recorded during 499 h of ground-based observations in Yellowstone National Park. All observed scent-marking (N = 158) was done by breeding wolves, primarily dominant individuals. Dominant breeding pairs provided most leadership, consistent with a trend in social mammals for leadership to correlate with dominance. Dominant breeding wolves led traveling packs during 64% of recorded behavior bouts (N = 591) and 71% of observed travel time (N = 64 h). During travel, breeding males and females led packs approximately equally, which probably reflects high parental investment by both breeding male and female wolves. Newly initiated behaviors (N = 104) were prompted almost 3 times more often by dominant breeders (70%) than by nonbreeders (25%). Dominant breeding females initiated pack activities almost 4 times more often than subordinate breeding females (30 vs. 8 times). Although one subordinate breeding female led more often than individual nonbreeders in one pack in one season, more commonly this was not the case. In 12 cases breeding wolves exhibited nonfrontal leadership. Among subordinate wolves, leadership behavior was observed in subordinate breeding females and other individuals just prior to their dispersal from natal packs. Subordinate wolves were more often found leading packs that were large and contained many subordinate adults.

Résumé : Nous avons analysé le comportement de commandement chez des loups gris (*Canis lupus*) reproducteurs et non reproducteurs appartenant à trois meutes durant les hivers de 1997–1999. Le marquage d'odeurs, la position en tête de meute (la durée et la fréquence au cours des déplacements), l'initiation des activités et la prise de décisions ailleurs qu'en tête du groupe ont été notés pendant 499 h d'observations au sol dans le Parc national de Yellowstone. Tous les marquages (N = 158) ont été faits par des loups reproducteurs, surtout des individus dominants. Ce sont surtout les couples dominants qui assurent le commandement, en accord avec une tendance chez les mammifères sociaux chez lesquels la fonction de chef est en corrélation avec la dominance. Les loups reproducteurs dominants ont conduit les meutes en déplacement pendant 64 % (N = 591) des épisodes de comportement et pendant 71 % des épisodes de déplacement (N = 64 h). Les mâles et les femelles reproducteurs ont dirigé les meutes en déplacement à peu près également, ce qui reflète probablement l'investissement parental important aussi bien de la part des reproducteurs mâles que des femelles. Les comportements nouveaux (N = 104) ont été adoptés presque trois fois plus souvent par des reproducteurs dominants (70 %) que par des individus non reproducteurs (25 %). Des femelles reproductrices dominantes ont été instigatrices des activités de leur meute environ quatre fois plus souvent que les femelles reproductrices subordonnées (30 vs. 8 fois). Bien qu'une femelle reproductrice subordonnée ait pris la direction de sa meute plus souvent que les individus non reproducteurs au cours d'une saison, cela n'est pas habituel. Dans 12 cas, des loups reproducteurs ont pris la direction de leur meute sans être en tête. Chez les individus subordonnés, le comportement de commandement a été observé chez des femelles reproductrices et chez d'autres individus juste avant qu'ils ne quittent leur meute d'origine au moment de la dispersion. Les loups subordonnés mènent surtout de grands troupeaux qui comptent beaucoup d'individus subordonnés.

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Introduction

In social groups or packs of gray wolves, *Canis lupus*, dominant individuals are those that successfully control the behavior of others (Schenkel 1947) and pack leaders are those that control pack movements (Mech 1970, p. 73, 2000; Boinski 2000). How pack leadership relates to dominance and breeding is not well documented for wild wolves, particularly in packs containing more than two breeding individuals (6–8% of all packs; Mech 2000). Furthermore, there is disagreement in the literature about the relative roles of male and female breeding wolves in directing pack activities. Murie (1944) referred to the dominant, or alpha, male as the lord and master of the pack; Haber (1977) agreed, and Fox (1980, p. 128) described the alpha male as *the* leader of the pack (italics added). Yet Mech (1966) and Peterson (1977) reported that the dominant female usually leads a pack during travel, at least during the midwinter breeding season. Mech (1970) referred to the dominant male as the one who initiates and guides attacks on intruding wolves from outside the pack. A recent review emphasized that it is alpha male wolves that are the pack leaders (Holekamp et al. 2000).

While it is generally understood, especially from studies of wolves in captivity (e.g., Fox 1980; Zimen 1981), that in wolves, leadership has some relationship to dominance and breeding status, quantitative data on leadership behavior in the wild have been reported for only one pack in summer (Mech 2000). Mech (1999) asserted that the significance of dominance relationships within pack society has been overrated, and he argued that wolf packs are best understood as family groups in which a breeding pair "shares leadership in a division of labor system in which the breeding female initiates pup care and the breeding male leads in foraging and food provisioning". According to this view, breeding wolves provide leadership because offspring tend to follow their parents' initiative. Yet we know little about how leadership roles might change in packs with multiple breeders (Mech 1999), or how individual age or pack size might influence the process of leading.

The primary objective of this study was to document and compare the leadership roles of breeding and nonbreeding wolves, dominant and subordinate breeding females, and dominant males and females. The reintroduction of wolves to Yellowstone National Park in 1995, following their extirpation by 1926 (Bangs and Fritts 1996; Bangs et al. 1998), afforded an opportunity to observe the behavior of wolves of known sex and age in free-ranging wild packs. We studied leadership behavior in three packs, including one with a simple structure (a breeding pair and their offspring) and two with multiple breeding females. All three packs contained offspring from multiple years. During the study there were two turnovers in dominant breeding individuals, shedding further light on the relationship between social status and leadership role.

Study area

The study was conducted on the 100 000-ha Northern Range of Yellowstone National Park in northwestern Wyoming and adjacent Montana (Houston 1982). Elevation ranges from 1610 to 3462 m (Yellowstone National Park 1997). The climate of the study area is characterized by long cold winters and short cool summers (Yellowstone National Park 1997). Forests in the area consist primarily of lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziezii*), but there are extensive open habitats that include mesic meadow, mesic shrub–meadow, riparian areas, grassland, sage grassland, and road (Weaver 1978; Gese and Grothe 1995). Our observations were made in open sagebrush–grassland and semi-open Douglas-fir steppe in the northeastern portion of the Park. The average temperature was –12°C during data collection in early winter (November–December) and –10°C during late winter (March). Although elk (*Cervus elapus*) were the primary prey of wolves during this study (Smith et al. 1999), other potential prey in the area included mule deer (*Odocoileus hemionus*), moose (*Alces alces*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), pronghorn antelope (*Antilocapra americana*), and mountain goat (*Oreamnos americanus*). Sympatric carnivores were primarily coyote (*Canis latrans*), mountain lion (*Puma concolor*), red fox (*Vulpes vulpes*), grizzly bear (*Ursus arctos*), and black bear (*Ursus americanus*). Many of the wolves we observed were originally translocated to Yellowstone National Park from British Columbia and Alberta, then held in acclimation pens for 10 weeks before being released in the Park (Phillips and Smith 1996).

Methods

Leadership data were recorded during ground observations made between September and March in 1997–1999. Behavioral evidence of leadership in gray wolves has not been systematically evaluated, so we selected five plausible behavioral indicators of leadership that were observed regularly in the field: scent-marking; frequency and time in the lead while packs were traveling or hunting (frontal leadership); initiation of pack behavior; and nonfrontal leadership. Scent-marking was included as a metric of leadership because it is an integral component of travel and dominance expression (Peters and Mech 1975). Observations were made using binoculars and spotting scopes up to 75× power from an average distance of 1 km. When packs traveled out of visual range, radiotelemetry was used to locate them and confirm the presence of breeding individuals.

Data were collected during September through mid-January and late January through March. Complete field seasons included early and late winter in 1997–1998 and 1998–1999, as well as early winter 1999. Included in both seasons were 30-day periods of daily tracking and observations beginning on 15 November and 1 March. All three packs observed in this study were frequently visible from a road that provided access for teams of two observers per pack.

All three packs were formed as wolf pairs initially reproduced in Yellowstone National Park in 1995 or 1996. Individual wolves in the three study packs were identified by the presence or absence of a radio collar and by distinctive pelage and other physical characteristics. The Rose Creek pack contained 14–23 wolves (mean 19.0) and the Leopold pack and Druid Peak pack included 8–13 (mean 10.4) and 7–8 (mean 7.8) wolves, respectively. The average numbers of pups and older subordinate nonbreeding wolves were 8.6

and 8.0 for the Rose Creek pack, 4.0 and 4.6 for the Leopold pack, and 3.0 and 2.6 for the Druid Peak pack, respectively. Pack size changed little during this study, but the number of nonbreeding yearlings and older wolves was generally greater during the second year of the study. The Leopold pack had a single breeding pair, the Rose Creek pack had two breeding females (mother and daughter ≥3 years apart in age), and the Druid Peak pack had two breeding female siblings, after a third breeding female sibling dispersed in November 1997. In the Druid Peak pack, one sister became dominant even though the other initially reproduced first. All breeding individuals were either radio-collared or easily distinguished from other wolves. Dominant individuals were identified from body postures such as raised tail and direct stare with ears forward, or because they elicited submissive responses from other wolves (Schenkel 1947, 1967). Dominant wolves were never observed exhibiting submission to other wolves. Breeding wolves, whether dominant or subordinate, were identified as such because they were seen copulating in winter or with newborn pups the following spring. Once a subordinate breeding female was identified in a pack, the pack was considered to have multiple breeders as long as she was present. Breeding females often shared whelping dens, so it was not always possible to determine individual reproductive success. No subordinate breeding males were detected during the study. However, because it was impossible to observe the wolves constantly, additional subordinate breeding males and females (if they did not whelp) could have been present without our knowledge.

Behaviors classified as scent-marking included raised-leg urination, scratching, and double scent-marking (Peters and Mech 1975). A double scent mark was recorded when two wolves in quick succession marked the same location.

During this study all three packs were highly cohesive. Individual subordinate wolves did separate ($N = 9$) temporarily or permanently from their pack, but packs rarely split into two or more groups. Data on frequency and time individual wolves led packs were collected only when the positions of both dominant breeding wolves in a pack were clear during the observation. A leadership bout was defined as a period when any individual wolf was identified at the head of the line during travel or pursuit of prey. A new bout began with a change in leading wolf or activity. Recorded for each bout were date, total duration, breeding and social status of the leading wolf (dominant breeder, subordinate breeder, or nonbreeder), pack identity, pack size, position of breeders, activity, and snow condition. Snow was classified by depth on the front legs of wolves: low or high if below or above the midpoint on the radius, respectively.

"Activity initiation" occurred when one wolf prompted the following: arousing the pack from rest, traveling after group rallies (greeting ceremonies), chasing prey, changing direction during travel, or defending the pack from trespassing wolves. "Nonfrontal leadership" occurred when a wolf not in the lead broke ranks and led the pack in a new direction or activity.

Statistical methods

The data were classified to year, pack, activity (travel or pursuit of prey), season (early or late winter), and identity of the wolf first in line (dominant male, dominant female, subordinate breeder, or nonbreeder). Observations of wolves pursuing prey were too sparse for analysis. The observations were organized into a three-dimensional contingency table, the dimensions being season, pack, and social status/sex categories.

The scent-marking data were relatively sparse, so for each season we conducted a χ^2 test of homogeneity (Gibbons 1997) across packs to see if data pooling across packs was feasible. We then conducted χ^2 tests of equal cell proportions (Gibbons 1997) to determine if scent-marking events were equally distributed across social status/sex categories (Martin and Bateson 1993). If significant differences were found we conducted one-tailed sign tests (Gibbons 1997) to evaluate differences in scent-marking rates between dominant males and dominant females. The null hypothesis was $P = 0.50$ and the alternative hypothesis was $P > 0.50$, where P denotes the proportion of scent-marking events performed by the dominant male. The postulated alternative hypothesis was based on higher expectations of leadership derived from earlier studies, primarily done on captive animals (i.e., male > female and dominant > subordinate) (Fox 1980; Zimen 1981).

For analyses of frequency and time at the head of the line, data were used only from bouts during which the positions of both dominant breeding wolves were known. For the frequency data we fit a three-dimensional log-linear model, the effects being pack, season, and social class/sex. The pack and season main effects were not of interest, as they arose from differences in numbers of observations across packs and seasons. The social status/sex effect was of primary interest, as well as the two-way interactions pack × social class, pack × season, and season × social class. If these interactions were significant, pooling of data across packs and (or) seasons was precluded, and a significant interaction of social class with pack and (or) season indicated that behaviors varied across packs and (or) seasons. We fit the log-linear model containing all main effects and all two-way interactions and conducted tests of significance. In some cases there were no subordinate breeding females and this created structural zeroes (Agresti 1990) in the frequency table, which we incorporated into the analysis.

The log-linear model analysis tests for equal distribution of leadership across social classes, but there were typically several nonbreeders and in at least one case more than one subordinate breeding female. For each pack and season we tested for equal distribution of leadership across social classes while accounting for the number of wolves in each category. We computed the expected leadership frequency based upon the null hypothesis of equal leadership distribution across wolves. The expected frequencies (E) were computed as follows: E = (number of wolves in category/total number of wolves in categories being compared) × total number of bouts for the categories being compared. The observed and expected frequencies were then compared using a χ^2 test. Note that the nature of the scent-marking data did not require this adjustment.

For each pack and season we first tested for equal distribution of leadership across wolves in all social classes. For nonbreeding wolves we included yearlings and adults but excluded pups (in this study pups led 3% of travel bouts).

Table 1. Frequency of scent-marking behavior (N = 158) observed in three free-ranging packs of gray wolves (*Canis lupus*) in Yellowstone National Park, Wyoming, in early winter (November–December) and late winter (March) of 1997–1999.

	Leopold pack	Rose Creek pack	Druid Peak pack	Total
Early winter				
Dominant pair	13	15	37	65
Dominant male	6	6	12	24
Dominant female	0	5	11	16
Other wolves	0	0	3	3
Late winter				
Dominant pair	5	5	5	15
Dominant male	14	15	4	33
Dominant female	1	1	0	2
Other wolves	0	0	0	0

Including pups could have biased the comparison between breeders and nonbreeders, owing to the age discrepancy. If we found a significant difference across classes, we proceeded to compare the dominant breeding male and dominant breeding female. There is only one dominant breeding male and one dominant breeding female in each pack, so their leadership rates were compared using a one-tailed sign test. In those tests we used only data from those two animals. We also compared frequency of leadership between the dominant breeding female and subordinate female breeders, accounting for the number of subordinate breeders. Before testing for differences between breeders and nonbreeders we compared subordinate breeding females with nonbreeders. In addition to frequency of leadership, proportion of time spent at the head of the line was calculated, to compare frequency of leadership between social classes and sexes of wolves.

For each set of hypothesis tests we controlled the overall level of significance at 0.05 using the Bonferroni procedure. Data for activity initiation and nonfrontal leadership were too sparse across packs and seasons for hypothesis testing, so we report only frequency of occurrence.

Results

Wolves were visible during 499 h of observation, representing approximately 30% of the winter observation periods. Leadership bouts (N = 591) comprised 64 h, two-thirds of which occurred in early winter and the remainder in late winter. Unless indicated otherwise, “breeder” refers to a dominant breeder, or alpha animal. Individual turnover was low, and pack composition did not fluctuate greatly during the study, so data were pooled across years for each pack. We could identify no influence of snow depth (relatively low in this study) on the tendency of breeders to lead ($\chi^2_{[1]} = 0.02$, $P = 0.89$), so results were pooled across snow categories.

The Leopold pack contained the same dominant breeding wolves in both years of the study. In the Druid Peak pack, the initial breeding male was illegally killed in early December 1997 and was replaced in the pack structure on 8 December by a male that dispersed from the Rose Creek pack. The dominant breeding female in the Druid Peak pack was the same individual (040) in both years of the study. In the Rose Creek pack, the dominant breeding male was the same individual (008) throughout the study, but the dominant breeding female (009) was replaced by her daughter (018) late in 1999 (early-winter study period in 1999). The breeding male (008) was not the father of the new dominant breeding female (018).

Scent-marking

We observed scent-marking 158 times, in all but 3 cases by dominant breeding wolves (Table 1). A subordinate breeding female in the Druid Peak Pack scent-marked 3 times in early winter by scratching when the dominant breeding male and female were not present. In 2 cases, subordinate females replaced dominant females that died or left packs, and the subordinate females initiated double scent-marking with the breeding male at about the same time they exhibited other dominant behavior.

For each season we found no significant differences in distribution of scent-marking events across social classes among the three packs (early winter: $\chi^2_{[6]} = 6.90$, $P = 0.33$; late winter: $\chi^2_{[4]} = 1.92$, $P = 0.75$), so we pooled the data across packs. In both early and late winter, scent-marking events were not evenly distributed across the four sex and social status classes (early winter: $\chi^2_{[3]} = 79.63$, $P < 0.0001$; late winter: $\chi^2_{[3]} = 55.4$, $P < 0.0001$)). In early winter, 65 of 108 (62%) of all observed scent-marking events involved both dominant males and females (Table 1) compared with 15 of 50 (30%) in late winter. In early winter the dominant males did not scent-mark significantly more often than the dominant females (24 vs. 16; sign test, $P = 0.11$) but did do so in late winter (33 vs. 2; sign test, $P < 0.0001$). While we acknowledge the possibility of bias in observing raised-leg urination by males versus females, because males tend to raise their legs somewhat higher, we infer nevertheless that participation in scent-marking by dominant female breeders declines between early and late winter relative to that of their male counterparts.

Leading during travel

The log-linear model analysis of leadership during travel indicated significant differences according to social class, and significant interactions between pack and social class, pack and season, and season and social class (all $P < 0.01$). This reflects a difference in frontal-leadership distribution across social classes according to pack and season. Consequently

Table 2. Frequency of leading during travel for wolves of different social classes in three free-ranging packs in early winter and late winter of 1997–1999 in Yellowstone National Park.

	Leopold pack				Rose Creek pack				Druid Peak pack			
	Early winter		Late winter		Early winter		Late winter		Early winter		Late winter	
	No. of bouts	No. of wolves	No. of bouts	No. of wolves	No. of bouts	No. of wolves	No. of bouts	No. of wolves	No. of bouts	No. of wolves	No. of bouts	No. of wolves
Breeding wolves												
Dominant males	25 (2.2)	3	19 (1.7)	2	25 (2.4)	3	35 (4.1)	2	72 (10.2)	3	23 (4.7)	2
Dominant females	23 (2.5)	3	10 (2.4)	2	17 (1.0)	3	20 (3.5)	2	98 (10.2)	3	13 (1.0)	2
Subordinate females	0 (0)	0	0 (0)	0	11 (2.1)	2	0 (0)	0	25 (1.6)	4	6 (0.5)	2
Nonbreeders	26 (1.7)	15	9 (0.6)	9	42 (3.9)	29	39 (3.4)	11	46 (4.0)	9	7 (0.7)	4
Total	74 (6.4)		38 (4.7)		95 (9.4)		94 (11.0)		241 (26.0)		49 (6.9)	

Note: Values show the number of observed leadership bouts and the number of wolves in the class; numbers in parentheses show the total time (h).

we conducted χ^2 tests for each pack and season, using a Bonferroni adjustment for the six tests while maintaining an overall level of significance of 0.05.

When the number of wolves in each social class was accounted for, we found significant differences between social class/sex categories for all packs and seasons (all $P < 0.001$): Leopold pack: early winter: $\chi^2_{[2]} = 47.9$; late winter: $\chi^2_{[2]} = 43.9$); Rose Creek pack: early winter: $\chi^2_{[3]} = 70.9$; late winter: $\chi^2_{[2]} = 57.7$; Druid Peak pack: early winter: $\chi^2_{[3]} = 178.5$; late winter: $\chi^2_{[3]} = 28.4$. We note that for three packs and seasons there were no subordinate breeding females. The travel-leading frequency of the dominant breeding male was not significantly greater than that of the dominant breeding female for any of the packs in any season (all $P > 0.05/6 = 0.008$ (critical value), Bonferonni procedure; minimum $P = 0.02$ for any single pack) (Table 2). The dominant breeding female led travel significantly more often than subordinate breeding females in the Druid Peak pack in early winter ($\chi^2_{[1]} = 68.1$, $P < 0.0001$), but not in the Rose Creek pack in early winter ($\chi^2_{[1]} = 0.01$, $P = 0.94$) nor in the Druid Peak pack in late winter ($\chi^2_{[1]} = 2.58$, $P = 0.11$).

Subordinate breeding females led significantly more often than nonbreeders only in the Rose Creek pack in early winter ($\chi^2_{[1]} = 17.96$, $P < 0.001$) (in other cases the differences were nonsignificant: Druid Peak pack in early winter: $\chi^2_{[1]} = 0.66$, $P = 0.42$; Druid Peak pack in late winter: $\chi^2_{[1]} = 0.96$, $P = 0.33$). We therefore pooled data for subordinate breeding females and nonbreeders for the Druid Peak pack tests when comparing breeders with nonbreeders. In all six pack/season comparisons breeders led significantly more often than nonbreeders (all $P < 0.0001$). Over all packs and seasons, breeders led for 78% of the recorded time (Table 2), ranging from a low of 58% (Rose Creek pack in early winter) to a high of 90% (Druid Peak pack in late winter).

When a large pack (Rose Creek) travels with many adults and subadults, pack size may influence individual roles, perhaps simply because more adults are present. In terms of both overall pack size and the number of subordinate nonbreeding yearlings and adults present, the packs were ranked as follows: Rose Creek > Leopold > Druid Peak. Within seasons (early and late winter), leadership provided by these social subordinates was similarly ranked (Table 2).

We were unable to fully evaluate the influence of experience and age on leadership because most dominant breeding wolves were several years old when packs formed simultaneously in Yellowstone National Park. However, we note that in the one case in which a dominant breeder was recruited from outside the pack, the newly arrived male tended to lead more than any other wolf observed in this study (Table 2), perhaps showing an assertiveness similar to the higher rate of scent-marking documented for newly formed wolf pairs (Rothman and Mech 1979).

Initiating behavior

When data were pooled across packs, pack activities were initiated 40 times by dominant breeding males and 30 times by dominant breeding females. Other wolves, especially subordinate breeding females, initiated activities 34 times. Over both seasons, breeding wolves initiated pack activities in 75% of the 104 observed cases (Table 3); 82% in early winter and 66% in late winter. In the Rose Creek pack, breeders

Table 3. Frequency of initiation of activity (*N* = 104), relative to sex and reproductive and social status, observed in wolves in three packs in early winter and late winter of 1997–1999 in Yellowstone National Park.

	Leopold pack		Rose Creek pack		Druid Peak pack	
	Early winter	Late winter	Early winter	Late winter	Early winter	Late winter
Breeding wolves						
Dominant males	12 (0.57)	11 (0.40)	4 (0.45)	2 (0.15)	7 (0.26)	4 (0.57)
Dominant females	3 (0.14)	8 (0.30)	1 (0.11)	3 (0.23)	15 (0.56)	0
Subordinate females	—	—	3 (0.33)	1 (0.8)	2 (0.7)	2 (0.29)
Nonbreeding wolves	6 (0.29)	8 (0.30)	1 (0.11)	7 (0.54)	3 (0.11)	1 (0.14)

Note: Numbers in parentheses show the proportion of total observation time for each pack.

(including subordinate breeding females) initiated behavior less often (64%, *N* = 22) than in the smaller packs (71% in the Leopold pack, *N* = 48; 88% in the Druid Peak pack, *N* = 34).

Nonfrontal leadership

Nonfrontal leadership was not commonly observed and often difficult to identify. Of the 15 cases recorded, all but 1 occurred with a nonbreeder at the head of the line. One nonbreeding male in the Leopold pack (055M) exhibited nonfrontal leadership 3 times during the winter prior to dispersing from the pack; otherwise all such observations were of breeding individuals. All other observations were of breeding wolves of both sexes who displayed leadership from a nonfrontal position.

Discussion

Several of the aspects of wolf behavior measured in this study seemed, a priori, to be linked to individual leadership potential. These metrics were variously successful. Nonfrontal leadership was rarely recorded and so contributed little to our understanding of individual roles. Initiation of pack behaviors was also infrequently observed, but our observations were consistent with the larger sample of individuals leading packs during travel.

Scent-marking, while having no direct bearing on leadership per se, provided the clearest indicator of dominant, breeding status, and our direct observations confirmed earlier work (Peters and Mech 1975; Haber 1977; Rothman and Mech 1979; Asa et al. 1990; Asa and Mech 1995; Mech 1995, 1999). All scent-marking was done by wolves of high status, and even a single observation of double scent-marking was sufficient to identify a wolf pair as dominant breeders. In this study, nonbreeders never marked, nor did most subordinate breeders; the only exception involved a female ascending to dominant status, who was observed scratching in the absence of the dominant pair. In another study, a female also ascending to dominant breeder status was seen flexed-leg urinating (Mech 1995).

The differences in scent-marking frequency between dominant males and females may be due to the apparent function of scent-marking in forming and maintaining a strong pair bond just prior to estrus. Dominant males marked at a high rate in both early winter and late winter, but dominant females seemed to mark less in late winter, after breeding ceased. Perhaps female scent marks function partly to indicate approaching receptivity. And the dominant male may maintain a higher level of territorial vigilance than the dominant breeding female, commensurate with his more extensive movements during the pup-rearing season (Mech 1999). We interpret differences in the scent-marking behavior of dominant breeding males and females as reflecting role differences relating to reproduction, not as differences in leadership.

The relative frequency that different individuals were recorded leading the pack during travel corresponded well to total time spent in the lead. Only the former data lent themselves to statistical analysis, which confirms the important role of breeding wolves, especially dominant breeders, in leading packs and prompting pack activities. We observed the highest frequency of leading by nonbreeding wolves in the Rose Creek pack, with 14–23 members. It is not clear whether this is a general pattern for large packs or simply an idiosyncrasy of the Rose Creek pack. In this study, variation in wolf leadership roles among packs was significant, consistent with the individual variation that is evident in virtually all studies of wolf behavior in captivity (e.g., Rabb et al. 1967; Zimen 1981; Fox 1971). Further work is necessary to determine whether large pack size reduces the almost exclusive tendency of dominant breeding wolves to lead smaller packs.

The strongest predictor of leadership in this study was high social rank, consistent with this general tendency previously identified for species with a strong hierarchical structure (Holekamp et al. 2000). Our findings should help resolve a continuing misperception, evident in the literature, that wolf packs are led by a single alpha wolf, the dominant male (Holekamp et al. 2000). Rather, a high-ranking male and female typically form the primary breeding pair and provide most leadership. In the case of gray wolves, contrary to the usual pattern for mammals, parental investment by both males and females is high, dominance within a pack is shared by the sexes, and pack-leadership responsibilities are shared by the sexes (Mech 2000). A similar pattern is seen in many species of social primates (Boinski 2000).

The results of this study suggest that individual variation in leadership patterns among wolf packs may be high and may vary with the season. We found division of leadership to be about equal between dominant males and females, at least in winter, in contrast to the pup-rearing season, when the male concentrates on travel and prey capture and the female is focused on rearing pups (Mech 1999). Individual variation may explain the occasional predominance of one wolf in leading the pack. Individual differences in age, experience, previous alliances, and temperament might influence ability to lead, but these influences have been poorly documented, even for social primates, which have been studied extensively (Boinski 2000).

Although dominant breeding wolves provided most leadership, we found that subordinate wolves, both breeders and nonbreeders, also provided leadership during travel. Dominant breeding wolves might share leadership in order to take advantage of pooled experience in a territory, although in this study a newly arrived dominant male showed the greatest tendency to lead. Shared leadership might reduce the energy expenditure of dominant individuals, such as in deep snow. Shallow snow prevailed in this study and we were unable to evaluate whether switching of leadership roles might increase with the cost of travel, which seems plausible. The ecological cost of travel for a 23-kg wolf was calculated to be 16% of daily energy expenditure (Steudel 2000), and this proportion would be higher for gray wolves, like those in Yellowstone National Park, that weigh twice this amount. Finally, shared leadership might spread the risks associated with travel, such as encountering fast water or thin ice. In two of the three packs in this study, the tendency of dominant females to lead declined in late winter, after the annual breeding season, when they are usually pregnant.

We caution against attaching undue significance to our observation that subordinate wolves sometimes led packs. Even though the subtle social interactions involved in travel coordination are difficult to observe, we found that dominant breeding wolves often made decisions that affected the pack's direction even when not in the lead. It is common in social species for subordinate individuals to closely monitor dominant leaders, so it is necessary to distinguish decision-makers, the true leaders, from initiators, who merely suggest a direction (Byrne 2000).

While two of the three packs in this study included multiple breeding females, relatives of the dominant breeding female, none of the packs had multiple male breeders that we knew of. This may be a general pattern that allows genetic relatives to participate in reproduction or ascend to dominant status. There is more uncertainty in determining genetic ties involving males than females, which perhaps explains the virtual absence of published records of multiple male breeders in a wolf pack. Persistence of subordinate female breeders in a pack appears to be at the discretion of the dominant breeding female. When subordinate females are allowed to remain within packs, their behavior (or, in this study, their role in pack leadership) appears to be tightly constrained by the dominant female breeder.

We have not used "alpha" because the value of this label has been questioned. Mech (1999) argued that the dominance hierarchy on which the structure of typical wolf packs containing a single breeding pair is based merely reflects parent–offspring dominance. However, in packs with multiple breeders, Mech (1999) allowed that there might be "intense rivalries such as those Haber (1977) reported" and that "the one use we may still want to reserve for 'alpha' is in the relatively few large packs comprised of multiple litters". Similarly, we found consistent differences in the roles played by dominant and subordinate female breeders. Dominant threats from the breeding pair usually prevent breeding by auxiliary wolves (Mech 1970; Peterson 1977), and indeed, the evolution of dominance behavior within wolf packs with multiple breeding females may be a result of selection pressure to adjust pack reproduction to food availability (Zimen 1976). Because wolves are usually food-limited, dominance relationships channel reproductive efforts into a single pair. As short-hand for "dominant breeder", "alpha" does seem to be appropriate for packs of multiple breeders. However, it falsely implies a hierarchical system in which each wolf assumes a place in a linear "pecking order" (Mech 1999).

We observed incipient leadership behavior in a subordinate male (nonfrontal leadership) just prior to dispersal and, with better documentation, among subordinate breeding females in the form of low-level scent-marking (when dominant wolves were absent), leading the pack, and initiating pack behaviors. A subordinate breeding female, related to the dominant female and her potential successor, may exhibit limited leadership and thus provide in the future a more successful transition in pack leadership that enhances matrilineal genetic survival.

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