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I examine leadership in Wolf (*Canis lupus*) packs based on published observations and data gathered during summers from 1986 to 1998 studying a free-ranging pack of Wolves on Ellesmere Island that were habituated to my presence. The breeding male tended to initiate activities associated with foraging and travel, and the breeding female to initiate, and predominate in, pup care and protection. However, there was considerable overlap and interaction during these activities such that leadership could be considered a joint function. In packs with multiple breeders, quantitative information about leadership is needed.

Key Words: Wolf, *Canis lupus*, leadership, behavior, foraging, movements, pup care, provisioning, sociality, reproduction, breeding, Northwest Territories.

Leadership in Wolf packs has been addressed only a few times. Mech (1970:73) defined leadership among Wolves as "... the behavior of one Wolf that obviously controls, governs, or directs the behavior of several others" such as when Wolves decide on direction of travel, when to rest or travel, and whether to chase prey. Peterson (1977) and Haber (1977) adopted similar definitions.

However, few opportunities have existed for studying leadership in wild Wolf packs because of the elusive nature of Wolves. Only Murie (1944), Clark (1971), Haber (1977), and Mech (1988, 1995a, 1999) have studied behavior in free-ranging Wolf packs, and no one has examined the leadership concept critically or quantitatively. This article attempts to do so, based primarily on my 13 summers of observation of a free-ranging Wolf pack.

Because Wolf packs are basically families (Murie 1944; Mech 1970), or at least almost always include a breeding pair (Mech and Nelson 1990; Mech et al. 1998), it is only natural that some member of this pair would be the pack leader (Mech 1970). This is because most members of the pack would be the offspring of the breeding pair and would tend to follow their parents' initiatives. Sometimes, a post-reproductive animal remains with the pack (Mech 1995a). Conceivably, such an individual, being older and more experienced, would lead in some activities. On the other hand, deposed breeders usually become subordinate, and tend not to take initiatives involving the group (Zimen 1976). A post-reproductive female on Ellesmere was subordinate to the breeding pair (Mech 1999).

Therefore, determining which member(s) leads the pack in a given activity would usually involve determining whether it is the breeding male or breeding female. Murie (1944) identified a male "lord and master" of a pack to which all four other

adults submitted. Murie concluded that this animal was not mated to any of the females, although there was no way he could have known (Haber 1977). One of the other adult males tended to lead the chases of Caribou, *Rangifer tarandus*, during Murie's study.

On Isle Royale, Mech (1966) observed from the air that in a large pack one member stood out as leading the pack, taking the initiative during hunts, and making decisions, but Mech could not identify the individual well enough to know whether it was always the same Wolf. It did, however, seem to be a male, and during the breeding season, a female sometimes led, with a male close behind her.

Later, Jordan et al. (1967) recognized a particular male that led the Isle Royale pack during travels for several winters. On the other hand, Peterson (1977), observing the Wolves during the breeding season, believed that females tended to lead the packs, as concluded by Pulliainen (1965: 236) who cited anecdotal literature.

Haber (1977) considered a "beta male" to be the leader of the Savage Pack in Denali Park. That animal tended to break trail, set the direction and pace of travel and resting, and initiated and ended most of the hunts and rest periods. However, this pack was highly unusual in that both the alpha male and beta male remained with the pack until 8 or 9-years old. No one else has ever reported two adult males remaining concurrently with a pack for even 4 years, including during a study of 13 packs for 4–9 years in the same area (Mech et al. 1998). In two other packs, Haber believed that high-ranking males generally led pack travels. During summer, leadership was less clear but Haber believed it also tended to involve high-ranking males. None of these studies provided quantitative behavioral data on leadership.

Methods

I gathered both quantitative and anecdotal data relevant to leadership from a free-ranging Wolf pack during summers 1986 through 1998 on Ellesmere Island, Northwest Territories, Canada (80°N, 86°W). There, Wolves prey on Arctic Hares (*Lepus arcticus*), Muskoxen (*Ovibos moschatus*), and Peary Caribou (*Rangifer tarandus pearyi*), and live far enough from exploitation and persecution by humans that they are relatively unafraid of people (Mech, 1988, 1995a). During 1986, I habituated the pack of Wolves there to my presence and reinforced the habituation each summer. The pack frequented the same area each summer and usually used the same den or nearby dens. The habituation allowed an assistant and me to remain with the Wolves daily, to recognize them individually, and to watch them regularly from as close as 1 meter (Mech 1988, 1995a, National Geographic 1988). We recorded all the behavior we observed, and the following results are based on all our observations, rather than on a sample. They do, however, apply only to the pack and period studied.

Results and Discussion

Awakening and Initiating Foraging

Discerning leadership in activities preceding travel away from the den was complex. Usually the activities included awakening of individuals, their awakening of packmates, considerable socializing, and eventually travel away from the den. Even after travel began, the trip could be aborted kilometers away when a pup or pups followed, and the breeding female eventually led or carried them back to the den.

Generally pack members awaited the awakening of their parents before becoming very active, although sometimes their activity would awaken the parents. Nevertheless, it was not until the parents were awake and active that much socializing went on. Often the breeding female awoke first and tried to awaken the male. Furthermore, the female sometimes seemed to urge the male to become active and go foraging. She would lead the male away only to have him lie down again, and the two would then begin howling. After that, the two would arise and go off again, but sometimes they would repeat this behavior a few times. Eventually the pair would leave the area, and after 5 to 30 minutes the female often returned alone, as Murie (1944) also observed, apparently having sufficiently motivated the male well enough to trust that he was actually continuing on. (On the other hand, the female of another pair I observed without offspring often ignored the howling of her mate when he behaved as though he wanted to depart from a foraging area. Rather than join the standing, restless, howling male, this female would continue resting or sleeping without even

replying to his howl. For example, at 2215 hours on 6 July 1998, this male howled 48 times with no reply from the nearby female.) Each summer, as the pups got older, the female tended to accompany the male and the rest of the pack for much longer periods. Of 29 times that I was able to determine which Wolf led the Ellesmere pair or pack away from the den, the male was first 22 times and the female 7 ($\chi^2 = 4.22$; $P < .05$; 1 d.f.).

Traveling

Discerning a leader during travel can be complicated by such issues as youthful exuberance and estrus that may cause individuals that might not be directing the overall activity to sometimes surge to the head of the line of traveling Wolves. Wolves often follow river beds, game trails, and old roads. When doing so, it is obvious where the pack is headed for certain stretches, so any Wolf may forge ahead temporarily, as Murie (1944) and Haber (1977) also noted.

During the breeding season, the order of a Wolf in line as the pack travels would be influenced by the fact that the breeding female would be in estrus. Thus the breeding male generally would be behind the breeding female both to guard her from other males and to be ready for breeding (Mech 1966: 61; Peterson 1977: 71-74).

On Ellesmere Island, I followed traveling Wolves during summer (Mech 1994). Because it was often difficult to navigate the terrain and remain close to the Wolf pack, I could not always identify the first Wolf in line during their travels. Therefore, I restricted my data collecting on this subject to times when I could.

On 70 occasions when I recorded which Wolf was ahead during actual travel, the male was ahead 46 times and the female 24 ($\chi^2 = 3.54$; $P = 0.06$). Most of these travel instances were observed in 1993, when the male led 27 times and the female 8 ($\chi^2 = 5.50$; $P = 0.02$), and 1996, when the male led 14 times and the female 12 (n.s.). In 1993, there were no pups, so the pack was comprised of the breeding pair and three yearlings. The yearlings food-begged and deferred far more to the male that year than to the female (Mech 1999). In 1996, the only adult-sized Wolves were the breeding pair.

Hunting

During attacks on prey, it is the breeders that seem to initiate and press the attack. Murie (1944) documented that it was high-ranking males, and Mech (1966) showed that it was those at the head of the pack, which usually are the breeders, that led the attack on Moose (*Alces alces*) and that both parents led attacks on Muskoxen (Mech 1988; National Geographic 1988). Clark (1971) found the same for Wolves hunting Caribou. Haber (1977) stated that high-ranking males tended to lead chases most

often. Ballard et al. (1987, 1991) found that adults, especially males, led the hunts. This was also true of Coyotes (*Canis latrans*) (Gese and Grothe 1995).

Whether the breeding male or breeding female begins the attack or predominates during it probably depends on the quickly changing circumstances of a given pursuit or attack. I have known of, or observed, cases in which both breeding male and breeding female in the absence of the other have killed ungulates. Furthermore, it seems reasonable to think that any experienced member of the pack that has an opportunity to initiate an attack might do so, as Clark (1971) observed, but that ordinarily the breeders would be in the best position to initiate an attack if all of the pack members are together.

During pack hunts of Arctic Hares on Ellesmere Island, all pack members chased hares when they had an opportunity. However, during hare hunts that lasted hours and involved many hares (usually leverets), the breeding male more often ambushed and caught hares chased by the yearlings. In 1993, I watched him capture four leverets this way and relinquish them to the yearlings, whereas I only saw the breeding female catch two during the same hunt, and she tried to eat them herself (Mech 1995b).

Provisioning the Pack

Provisioning the pack includes not only hunting, as discussed above, while the pack is nomadic during fall, winter, and spring, but also delivering food to the female and pups around the summer den and rendezvous sites. The breeding male clearly dominates this activity during the first several weeks after the pups are born, for the female remains with the pups most of that time and depends considerably on the male for her own food (Mech et al. 1999). As the male approaches the den, the female rushes him solicitously. If the male is carrying food, he drops it, or the female snatches it away from him with his clear consent. If the food is in his stomach, the male regurgitates, and the female instantly consumes the regurgitant.

When the pack has no pups, then the male plays a major role in feeding the yearlings (Mech 1999). I once watched the breeding pair leave three yearlings at their rendezvous site and travel 9.5 km away, where the male then dug up a cached Muskox calf shoulder and delivered it to the breeding female. She consumed it and then immediately returned to the yearlings and regurgitated to them (Mech 1995b). This behavior appeared to be merely an extension of the breeding male's behavior of feeding the female while she tends the pups.

However, provisioning the breeding female when she is caring for the pups is a difficult activity to assess for determining leadership (Mech 1999). Is the breeding male showing leadership because he hunts and brings food back to the breeding female? Or is the breeding female displaying leadership

because she takes charge of the food from the breeding male?

Contending with Intruders at Den

During disturbances at the den, it is difficult to determine which Wolf might be leading activities because of the general turmoil by all pack members. Murie (1944) described several instances in which a pack chased Grizzly Bears (*Ursus arctos*) away from the East Fork den, and generally the high-ranking (older) males were the most aggressive and persistent. This was also true when Murie himself disturbed the Wolves. As indicated earlier, Clark (1971) observed that the breeding female was most likely to drive away intruders, but Haber (1977) observed that with his packs it was usually the alpha male.

I made one observation of the Ellesmere pack protecting their den from a disturbance in 1994 that sheds some light on the subject. The pack consisted of a breeding pair, one 2-year-old male offspring, a 2-year-old female offspring, and one 5-week old pup. All were asleep around the den when an adult male Muskox wandered over a nearby ridge to the den area. The breeding male, which was farthest away, sensed the animal first and approached it. After a flurry of activity when the others detected the Muskox, the intruder stood its ground around the den. All the Wolves excitedly circled it and approached it many different times while it stood its ground in front of the den entrance with the pup inside.

After about 1 hour, during which the pack was unsuccessful in forcing the Muskox to leave, the breeding female began barking and bark-howling. All pack members then followed her to the west of the den and Muskox, where they all sat or lay while the breeding female continued barking and bark-howling. They were positioned about 5 meters apart, with the breeding female being closest to the Muskox but still 10 meters away.

It appeared that the breeding female had suddenly realized that surrounding the Muskox was only keeping it in front of the den, so she had led the pack to one side, giving the Muskox a safe direction away from the den. After 30 minutes of the Wolves remaining to one side of the den with the breeding female bark-howling, the Muskox headed eastward away from the den. The Wolves then returned to the den, and the pup emerged. During this incident, the breeding female always approached the Muskox more closely than did the male, as she also did in a similar incident in 1996.

In five similar incidents, the male acted more aggressively toward the Muskox one time, and neither male nor female paid the Muskox much attention in the other four. With a disturbance by a strange human in 1996, the male responded most aggressively while the female led the pups away.

Interacting with Alien Wolves

I have watched breeding pairs of Wolves on Ellesmere encounter alien Wolves four times, and each time they pursued the stranger together and with apparently equal aggressiveness (Mech 1993 and unpublished). After another such encounter of which I only observed the aftermath, the breeding pair and the breeding female's post-reproductive mother were all bloody, indicating that all had participated in the attack, which ended in the death of an alien Wolf. Murie (1944) found that an adult male at a den was most aggressive towards an alien Wolf that approached, and Harrington and Mech (1979) found that it was the breeders, most often the adult male, which approached the source of strange howls.

Caring for Pups

As expected, breeding females take the initiative and clearly spend more time and effort caring for the pups than do any other pack members, even though the breeding male and all other Wolves that center around the den feed and play with them and show general concern for them (Murie 1944; Clark 1971; Haber 1977; Mech 1988; Ballard et al. 1991, Mech et al. 1999). However, the only Wolf I have ever seen carrying a pup was the mother, although I have observed a post-reproductive female attempting to do so.

Packs with Multiple Breeders

A relatively small proportion of free-ranging Wolf packs include multiple breeders. The number of pack years in which multiple females per pack produce pups are estimated at between 6% (Packard 1980) and 41% (Harrington et al. 1982). The higher figure, however, included a sample of gravid Wolves (Rausch 1967), some of which probably resorbed their fetuses eventually (Hillis 1990), and it did not include large samples of Wolf packs from studies that Packard (1980) surveyed. In Denali Park alone, where multiple litters have been much publicized (Murie 1944; Haber 1977), the actual incidence of multiple litters was 9 (8%) in 108 pack years (Mech et al. 1998).

Nevertheless, packs with multiple litters have been the subjects of three of the four observational studies of wild Wolf behavior, and in their complexity they could shed light on the simpler social structure of most packs. However, little is known about the relationships between the breeding pairs in such packs, except that most likely the female breeders are related, probably mother and daughter or mother and two daughters, with the daughters' mates being adopted males (Mech et al. 1998). Whatever the case, the breeding males are probably unrelated to their mates (Smith et al. 1997). An exception may be the Rose Creek pack reintroduced into Yellowstone National Park in 1995, in which the 2–3 breeding females during 1997 and 1998 most probably were

bred by related packmates (D. W. Smith, personal communication).

Unfortunately, no quantitative data about packs with multiple litters were obtained to allow any definite conclusions to be drawn about leadership in such packs (Murie 1944; Clark 1971; Haber 1977). One of the two breeding females Clark observed in the Nadluardjuk pack of Baffin Island dominated the other, but no other information about leadership in that pack was reported.

Conclusions

The above observations are consistent with the prevailing view that Wolf packs typically are family units, with the adult parents guiding the activities of the group and sharing group leadership in a division-of-labor system (Mech 1999) in which the female initiates primarily such activities as pup care and defense, and the male initiates primarily foraging and food provisioning and the travels associated with them. There is much overlap in the leadership activities.

Socially, the breeding pair dominate their offspring and lead their activities, and although the breeding male appears socially dominant to the breeding female (Mech 1999), he feeds the female while she nurses the pups and cooperates with her in their care and protection. As the pups age, the male seems more intent on feeding them than does the female, perhaps allowing the female to improve her nutritional condition for the next litter. Conceivably, once the female is in good enough condition, she might then contribute as vigorously to offspring provisioning as the male.

In packs with multiple litters, it seems likely that the original progenitors of the pack, being oldest, probably dominate and lead the pack. However, as the younger breeders age, they may assume more initiative and lead their own offspring independently. This is probably the best explanation for both temporary (Mech 1966; Jordan et al. 1967 but cf. Haber 1977) and permanent pack splitting (Mech 1986; Mech et al. 1998). More information about leadership in packs with multiple breeders is needed.

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