Alpha Status, Dominance, and Division of Labor in Wolf Packs

by
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Abstract: The prevailing view of a wolf (*Canis lupus*) pack is that of a group of individuals ever vying for dominance but held in check by the "alpha" pair, the alpha male and the alpha female. Most research on the social dynamics of wolf packs, however, has been conducted on non-natural assortments of captive wolves. Here I describe the wolf-pack social order as it occurs in nature, discuss the alpha concept and social dominance and submission, and present data on the precise relationships among members in free-living packs based on a literature review and 13 summers of observations of wolves on Ellesmere Island, Northwest Territories, Canada. I conclude that the typical wolf pack is a family, with the adult parents guiding the activities of the group in a division-of-labor system in which the female predominates primarily in such activities as pup care and defense and the male primarily during foraging and food-provisioning and the travels associated with them.

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Introduction

Wolf (*Canis lupus*) packs have long been used as examples in descriptions of behavioral relationships among members of social groups. The subject of social dominance and alpha status has gained considerable prominence (Schenkel 1947; Rabb et al. 1967; Fox 1971*b*; Zimen 1975, 1982), and the prevailing view of a wolf pack is that of a group of individuals ever vying for dominance but held in check by the "alpha" pair, the alpha male and the alpha female (Murie 1944; Mech 1966, 1970; Haber 1977; Peterson 1977).
Most research on the social dynamics of wolf packs, however, has been conducted on wolves in captivity. These captive packs were usually composed of an assortment of wolves from various sources placed together and allowed to breed at will (Schenkel 1947; Rabb et al. 1967; Zimen 1975, 1982). This approach apparently reflected the view that in the wild, "pack formation starts with the beginning of winter" (Schenkel 1947), implying some sort of annual assembling of independent wolves. (Schenkel did consider the possibility that the pack was a family, as Murie (1944) had already reported, but only in a footnote.)
In captive packs, the unacquainted wolves formed dominance hierarchies featuring alpha, beta, omega animals, etc. With such assemblages, these dominance labels were probably appropriate, for most species thrown together in captivity would usually so arrange themselves.

In nature, however, the wolf pack is not such an assemblage. Rather, it is usually a family (Murie 1944; Young and Goldman 1944; Mech 1970, 1988; Clark 1971; Haber 1977) including a breeding pair and their offspring of the previous 1-3 years, or sometimes two or three such families (Murie 1944; Haber 1977; Mech et al. 1998).

Occasionally an unrelated wolf is adopted into a pack (Van Ballenberghe 1983; Lehman et al. 1992; Mech et al. 1998), or a relative of one of the breeders is included (Mech and Nelson 1990), or a dead parent is replaced by an outside wolf (Rothman and Mech 1979; Fritts and Mech 1981) and an offspring of opposite sex from the newcomer may then replace its parent and breed with the stepparent (Fritts and Mech 1981; Mech and Hertel 1983).

Nevertheless, these variations are exceptions, and the pack, even in these situations, consists of a pair of breeders and their young offspring (Mech 1970; Rothman and Mech 1979; Fritts and Mech 1981; Mech and Hertel 1983; Peterson et al. 1984). The pack functions as a unit year-round (Mech 1970, 1988, 1995*b*).

As offspring begin to mature, they disperse from the pack as young as 9 months of age (Fritts and Mech 1981; Messier 1985; Mech 1987; Fuller 1989; Gese and Mech 1991). Most disperse when 1-2 years old, and few remain beyond 3 years (Mech et al. 1998). Thus, young members constitute a temporary portion of most packs, and the only long-term members are the breeding pair. In contrast, captive packs often include members forced to remain together for many years (Rabb et al. 1967; Zimen 1982; Fentress et al. 1987).

Attempting to apply information about the behavior of assemblages of unrelated captive wolves to the familial structure of natural packs has resulted in considerable confusion. Such an approach is analogous to trying to draw inferences about human family dynamics by studying humans in refugee camps. The concept of the alpha wolf as a "top dog" ruling a group of similar-aged compatriots (Schenkel 1947; Rabb et al. 1967; Fox 1971*a*; Zimen 1975, 1982; Lockwood 1979; van Hooff et al. 1987) is particularly misleading.

Because wolves have been persecuted for so long (Young and Goldman 1944), they have been difficult to study in the wild (Mech 1974) and therefore information about the social interactions among free-living wolf pack members has accumulated slowly. Little is known about the interactions between breeding males and breeding females under natural conditions, and about the role of each in the pack and how dominance relates to these relationships.

A few people have observed the social behavior of wild wolves around dens, but Murie (1944) gave an anecdotal account, Clark (1971), in an unpublished thesis, presented only a quantified summary of the pack's hierarchical relationships, and Haber (1977) described his interpretation of a pack's social hierarchy but gave no supporting evidence. Thus, no one has yet quantified the hierarchical relationships in a wild wolf pack.

Here I attempt to clarify the natural wolf-pack social order and to advance our knowledge of wolf-pack social dynamics by discussing the alpha concept and social dominance and by presenting information on the dominance relationships among members in free-living packs.

This study was conducted during the summers of 1986-1998 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, 1995*a*). During 1986, I habituated a 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 me and an assistant to remain with the wolves daily, to recognize them individually, and to watch them regularly from as close as 1 m (Mech 1988, 1995*a*; National Geographic Society 1988).

We noted each time a wolf submitted posturally to another wolf. Usually this deference was characterized by "licking up" to the mouth of the dominant animal in the "active submission" posture (Fig. 5 in Schenkel 1967), similar to that described by Darwin (1877) for domestic dogs. Often this behavior took place as an animal returned to the den area after foraging, and sometimes the returning individual disgorged food to the soliciting wolf (Mech 1988; Mech et al. 1999). Other behavior noted included "pinning," or passive submission (Schenkel 1967), in which the dominant wolf threatened another, which then groveled, and "standing over," in which one wolf stands over another, which often lies nonchalantly but in a few cases sniffs the genitals of the other. I did not consider "standing over" a dominance behavior (L.D. Mech, submitted for publication). [2]

The following is a summary of generalizations documented in the previous references, together with new quantified findings.

Alpha status

"Alpha" connotes top ranking in some kind of hierarchy, so an alpha wolf is by definition the top-ranking wolf. Because among wolves in captivity the hierarchies are gender-based, there are an alpha male and an alpha female (Schenkel 1947).

The way in which alpha status has been viewed historically can be seen in studies in which an attempt is made to distinguish future alphas in litters of captive wolf pups. For example, it was hypothesized that "the emotional reactivity of the dominant cub, the *potential* alpha animal (emphasis mine) of the pack, might be measurably different from the subordinate individuals," and that "it might then be possible to pick out the temperament characteristics or emotional reactivity of *potential alpha or leader wolves* (emphasis mine), and of subordinates" (Fox 1971*b*, p.299). Furthermore, "Under normal field conditions, it seems improbable that timid, low ranking wolves would breed" (Fox 1971*a*, p.307). This view implies that rank is innate or formed early, and that some wolves are destined to rule the pack, while others are not.

Contrary to this view, I propose that all young wolves are potential breeders and that when they do breed they automatically become alphas (Mech 1970). Even in captive packs, individuals gain or lose alpha status (Zimen 1976), so individual wolves do not have an inherent permanent social status, even though captive pups show physiological and behavioral differences related to current social rank (Fox 1971*b*; Fox and Andrews 1973). Secondly, wolves in captivity breed readily, and I know of no mature captive individuals that failed to breed when paired apart from a group, as would be the case if there were inherently low-ranking, nonbreeders.

Third, in the wild, most wolves disperse from their natal packs and attempt to pair with other dispersed wolves, produce pups, and start their own packs (Rothman and Mech

1979; Fritts and Mech 1981; Messier 1985; Mech 1987; Gese and Mech 1991; Mech et al. 1998). I know of no permanent dispersers that failed to breed if they lived long enough.

Wolves do show considerable variation in dispersal age, distance, direction, and other dispersal behavior (see references above), and conceivably these are related to the intralitter variation discussed above (Fox 1971*b*; Fox and Andrews 1973). However, unless a maturing pack member inherits a position that allows it to breed with a stepparent in its own pack (Fritts and Mech 1981; Mech and Hertel 1983), sooner or later it will disperse and attempt to breed elsewhere.

Labeling a high-ranking wolf alpha emphasizes its rank in a dominance hierarchy. However, in natural wolf packs, the alpha male or female are merely the breeding animals, the parents of the pack, and dominance contests with other wolves are rare, if they exist at all. During my 13 summers observing the Ellesmere Island pack, I saw none. Thus, calling a wolf an alpha is usually no more appropriate than referring to a human parent or a doe deer as an alpha. Any parent is dominant to its young offspring, so "alpha" adds no information. Why not refer to an alpha female as the female parent, the breeding female, the matriarch, or simply the mother? Such a designation emphasizes not the animal's dominant status, which is trivial information, but its role as pack progenitor, which is critical information.

The one use we may still want to reserve for "alpha" is in the relatively few large wolf packs comprised of multiple litters. Although the genetic relationships of the mothers in such packs remain unknown, probably the mothers include the original matriarch and one or more daughters, and the fathers are probably the patriarch and unrelated adoptees (Mech et al. 1998). In such cases the older breeders are probably dominant to the younger breeders and perhaps can more appropriately be called the alphas. Evidence for such a contention would be an older breeder consistently dominating food disposition or the travels of the pack.

The point here is not so much the terminology but what the terminology falsely implies: a rigid, force-based dominance hierarchy.

The degree to which these arguments apply to other species no doubt varies considerably and is beyond the scope of this article. However, it is notable that similar arguments might be made for African hunting dogs (*Lycaon pictus*), which ecologically are similar to wolves (Mech 1975). Whereas some workers observed no rank-order behavior in this species (Kuhme 1965; Estes and Goddard 1967), others liberally write of "alpha" animals (Creel and Creel 1996).

Dominance and submission among pack members

The concept, nature, and importance of the dominance hierarchy or pecking order (Schjelderup-Ebbe 1922) itself in many species are in dispute (summary in Wilson 1975). Similarly, in a natural wolf pack, dominance is not manifested as a pecking order and seems to have much less significance than the results of studies of captive packs had implied (Schenkel 1947, 1967; Rabb et al. 1967; Zimen 1975, 1982; Lockwood 1979). In a natural wolf pack, the dominance rules bear no resemblance to those of the pecking order, that of a group of similar individuals competing for rank.

The only consistent demonstration of rank in natural packs is the animals' postures during social interaction. Dominant wolves assume the classic canid standing posture with tail

up at least horizontally, and subordinate or submissive individuals lower themselves and "cringe" (Darwin 1877). In fact, submission itself may be as important as dominance in terms of promoting friendly relations or reducing social distance.

Schenkel (1967), who promoted the importance of submission, recognized two main types, active and passive. He believed that active submission is derived from food-begging behavior, and I find active submission and food-begging indistinguishable. The begging or submissive wolf approaches another wolf excitedly, wagging the tail, lowering the ears, and "licking up" to the other wolf. The other wolf may or may not regurgitate food, depending on circumstances (Mech et al. 1999). In passive submission, the submissive wolf rolls over on its side or back, and the dominant wolf sniffs its groin or genitals (Schenkel 1967). Active submission was more common in the Ellesmere Island pack.

In that pack, all members, including the breeding female, submitted posturally to the breeding male, both actively and passively (Schenkel 1967). The yearlings and 2-year-old wolves and one old post-reproductive female submitted to both breeders. These rules held regardless of pack composition: breeding pair or breeding pair with pups (Table 1); breeding pair with yearlings (Table 2); breeding pair with yearlings and pups (Table 3); breeding pair with pups and 2-year-old auxiliaries (Table 4), or breeding pair with pups and post-reproductive female (Table 5).

Table 1. Dominance interactions, i.e., the number of times individual wolves dominated others or were submitted to, during summer between breeders in the Ellesmere Island wolf pack when no auxiliaries were present.

Year	Breeding male	Breeding female	Pups present?
1992	9	0	Yes
1996	21	0	Yes
1998	4	0	No

Note: Interactions were primarily active submissions, but three cases of passive submission are included (Schenkel 1967); they do not include "standing over" or interactions involving food, except for "food-begging".

Table 2. Dominance interactions, i.e., the number of times individual wolves dominated others or were submitted to, among breeders and yearlings in the Ellesmere Island wolf pack in 1993 (no pups were present, and parents were as shown in Table 1).

□	Male parent	Female parent	Female yearling 1	Male yearling	Female yearling 2	Total
Male parent	--	0	0	0	0	0
Female parent	3	--	0	0	0	3
Yearling female 1	3	2	--	0	4	9
Yearling male	4	3	0	--	0	7
Yearling female 2	4	3	0	0	--	7
Yearling?	3	2	0	0	0	5
Total	17[a]	10[a]	0	0	4	31

Note: Interactions do not include "standing over" or involve food, except for "food-begging."

[a]For male parent versus female parent, χ^2=0.94, P = 0.33, df = 1.

Table 3. Dominance interactions, i.e., the number of times individual wolves dominated others or were submitted to, among breeders and yearlings in the Ellesmere Island wolf pack in 1988 (pups present and breeding male was the same, as in 1990-1996).

□	Male parent	Female parent	Male yearling	Female yearling	Total
Male parent	—	0	0	0	0

Female parent	2	—	1	0	3
Male yearling	8[a]	4	—	1	13
Female yearling	5[b]	9	0	—	14
Total	15	13	1	1	30

Note: Interactions do not include "standing over" or involve food, except for "food-begging."
[a]Includes one short bout of five submissions.
[b]Includes one short bout of four submissions.

Table 4. Dominance interactions, i.e., the number of times individual wolves dominated others or were submitted to, among breeders and 2-year-old wolves[a] in the Ellesmere Island wolf pack in 1994 (pups were present, and parents were the same as is shown in Tables 1 and 2).

□	Male parent	Female parent	Two-year-old female	Two-year-old male	Total
Male parent	—	0	0	0	0
Female parent	13	—	2[b]	2	17
Two-year-old female	8	9	—	4	21
Two- year-old male	4	0	0	—	4
Total	25[c]	9[c]	2	6	42[c]

Note: Interactions do not include "standing over" or involve food, except for "food-begging."
[a]These are the yearlings in Table 2.
[b]The female parent dominated the 2-year-old female for 15 min at one of these times. Another time, when it was unclear whether the female parent or 2-year-old female dominated, is not included.
[c]For male parent versus female parent, $\chi^2 = 3.99$, $P = 0.05$.

Table 5. Dominance interactions, i.e., the number of times individual wolves dominated others or were submitted to, among breeders and a post-reproductive female in the Ellesmere Island wolf pack in the summers of 1990 and 1991 (pups were present and the male parent was the same as in all other years in the study except 1998).

□	Male parent	Female parent[a]	Post-reproductive female[b]	Total
Male parent	—	1[c]	0	0
Female parent[a]	35	—	1	36
Post-reproductive female[b]	26	17	—	43
Total	61	18	1	80[d]

Note: Interactions do not include "standing over" or involve food, except for "food-begging."
[a]Yearling female in 1988 (Table 1) and female parent in 1990-1996.
[b]Female parent in 1988 and 1989 (Table 1).
[c]Male deferred when approaching a female and young pups in a den.
[d]$\chi^2 = 12.64$, $P < 0.001$, df = 1.

That these submission rules help promote friendly relations was demonstrated dramatically by an observation I made on 22 June 1991. A post-reproductive female returned to the den area with a very dried hare carcass, more an interesting distraction than food. Instead of bringing the dried hare directly to the pups, the old female went out of her way to take it submissively to the breeding male, which instantly snatched it from her. He refused entreaties by both that female and even the breeding female and chewed it himself for 20-30 min.

The only other general dominance rules I discerned involved scent-marking and food ownership and transfer. With scent-marking, both breeding male and female mark, but subordinates do not unless vying for dominance (Packard 1989; Asa et al. 1990), and I have seen no exceptions. Regarding food ownership and transfer, when the pack contained pups or yearlings, the breeding male I observed either regurgitated or dropped

food to his mate or allowed her to snatch it from him or he delivered it directly to his offspring.

Aside from these food deliveries, there appeared to be an ownership zone (Mech 1970) around the mouth of each wolf, and regardless of the rank of a challenger, the owner tried to retain the food it possessed, as Lockwood (1979) also found with captive wolves. Wolves of any rank could try to steal food from another of any rank, but every wolf defended its food (Table 6). Generally, dominant wolves seemed to succeed more at stealing food, but sample size was too small for a definite conclusion to be drawn.

Table 6. Observed attempts to defend food from packmates[a] in the Ellesmere Island wolf pack.

Date	Possessor of food	Challenger	Result
1988-06-26	Pups/yearling female[b]	Breeding female	Succeeded
1988-07-01	Yearling female Pup[c]	Breeding female Yearling male	Succeeded Failed
1988-07-05	Yearling female	Breeding female	Succeeded
1988-07-27	Yearling female Breeding male Breeding male	Yearling male Yearling female Yearling male	Failed Failed Succeeded
1990-08-05	Breeding male	Post-reproductive female	Failed
1991-06-22	Post-reproductive female	Breeding male	Succeeded
1993-07-11	Yearling female	Yearling female	Failed
1994-07-16	Pups and yearling male	Yearling female	Failed
1996-07-15	Pups/breeding female	Breeding male[d]	Succeeded
1998-07-07	Breeding female	Breeding male	Failed

[a]Does not include the breeding female taking food from the breeding male.
[b]Yearling female had brought food to the pups and snapped at the breeding female when she stole it.
[c]Yearling female, who had brought a hare, stood guard near the pup.
[d]Breeding female failed to stop the breeding male.

Two other behaviors among pack members could have been dominance-related, although data were insufficient to be certain. They were "standing over" and "hugging" (L.D. Mech, see footnote). In "standing over," one wolf would stand over (Schenkel 1947) a lying wolf, positioning its groin above the nose of the lying wolf. Sometimes the lying wolf sniffed at the groin or genitals of the standing wolf.

Schenkel (1947) saw "standing over" only during "peaceful" times and did not seem to consider it dominance-related. In the case of hugging, my sample size (5) was insufficient to determine whether it was dominance-related (L.D. Mech, see footnote).

The above dominance rules, which involve a natural age-based order with the current breeders at the top and offspring or non-breeders subordinate, are so automatic that they are seldom contested. In that respect, the social interactions among members of natural wolf packs are much calmer and more peaceful than Schenkel (1947) and Zimen (1982) described for captive wolves, as Clark (1971) also noted. Similarly, pups defer to adults and older siblings in the same automatic, peaceful way. When or whether a rank order develops among pups is in dispute (cf. Zimen 1975 and Fox and Andrews 1973; Haber 1977), and I cannot shed any light on that issue. Even among yearlings and 2-year-olds there were few rank displays (Tables 2-5).

It is conceivable that social tensions would mount during the breeding season (Schenkel 1947), but the fact that most natural packs contain only a single breeding pair would

preclude such tension. The earliest age at which wild wolves are known to breed is 22 months (Seal et al. 1979), and some individuals are not sexually mature until they are at least 4 years old (Haber 1977; Mech and Seal 1987). Because most wolves disperse before 2 years of age, and almost all before 3 years of age (Mech 1987; Gese and Mech 1991; Mech et al. 1998), there would be no source of sexual competition within most packs.

Thus, only in the relatively few packs with multiple breeders might there be intense rivalries such as those Haber (1977) reported during the breeding season in his unusual pack. On the other hand, at least some of the difference in reported "hostility" might be due to different viewpoints of the observers. I occasionally saw intense "pinning" of a 2-year-old female by her mother in summer 1994 that some might label "hostile." However, to me this behavior appeared to be merely the type of interaction I observed between the mother and an errant pup she could not control. In any case, these types of interaction were uncommon during my study.

As for high-ranking animals asserting any practical control over subordinates, the nature of the interaction is highly conditional. For example, with large prey such as adult moose (*Alces alces*), pack members of all ranks (ages) gather around a carcass and feed simultaneously, with no rank privilege apparent (Mech 1966; Haber 1977); however, if the prey is smaller, like a musk ox calf, dominant animals (breeders) may feed first and control when subordinates feed (Mech 1988; National Geographic 1988).

Similarly, pups are subordinate to both parents and to older siblings, yet they are fed preferentially by the parents, and even by their older (dominant) siblings (Mech et al. 1999). On the other hand, parents both dominate older offspring and restrict their food intake when food is scarce, feeding pups instead. Thus, the most practical effect of social dominance is to allow the dominant individual the choice of to whom to allot food.

The only other rank privilege I am aware of in natural situations is that high-ranking pups are more assertive in competing for food deliveries by adults and sometimes accompany adults on foraging trips at an earlier age than do subordinates (Haber 1977).

Dominance between the breeding male and female

The relationship between the breeding male and female is complex and bears further research. With captive packs there are contradictory claims regarding the dominance roles of "alpha males" and "alpha females" in relation to each other and to subordinates. This issue also relates closely to the concept of leadership but is not necessarily the same (L.D. Mech, submitted for publication).[1]

Whether each gender has its own dominance hierarchy has been subject of disagreement. As van Hooff et al. (1987, p.248) also noted, Schenkel (1947) and Zimen (1982) claimed that in captive wolves each gender has a separate hierarchy. However, in studies of wild wolves, the results tend to disagree. Clark's (1971) data indicated that the breeding male dominated all other wolves and the breeding female dominated all but the breeding male. Haber (1977, p.203) claimed that in the wild wolves he studied, males generally dominated, "with only a few exceptions." My data agree in that breeding males dominate posturally insofar as only once have I seen the breeding male defer posturally to the female (Tables 1-5).

The disagreement about the relationships between breeding males and females probably results from the great differences in pack composition and backgrounds between captive

and natural packs discussed earlier. Thus, it is useful to describe the typical interactions between breeding male and female in natural packs, as these interactions have not been described before.

When the breeding male and breeding female are separated, recognize each other, and then meet, the breeding female approaches the male in a typical subordinate posture: with the tail down or between the legs, body crouched or on the ground, ears back, and nose pointed up, and licking the male's mouth (Schenkel 1947). The male stands there nonchalantly, sometimes raising his tail horizontally.

During summers when the pack I observed had pups or yearlings, such a meeting most often took place near them, as the male was returning from foraging. His response to the female's greeting was to drop whatever food item was in his mouth and/or to regurgitate (Mech et al. 1999). The female then ate the food or gave it to the offspring. I could not distinguish greetings such as this that resulted in regurgitation from those that did not.

In 1998, when the breeding pair had no offspring, the four meetings of pair members that I observed each took place immediately after the female had been temporarily foraging separately or had been separately caching food from a kill. Each time the female returned to her mate, she assumed the active-submissive posture when she met the male, and one of these times she submitted profusely for about 90 s. Even once when the breeding female was intently chasing another wolf and was overtaken by her mate (17 June 1991), she submitted momentarily as the male passed her. It seems reasonable to conclude from these observations that the breeding female was subordinate to her mate.

The practical implications of this postural submissiveness, however, are not apparent. The behavior does not seem always to constitute food-begging. For example, during one 1998 meeting, the female postured toward the male as described above while she possessed a long bone from which she had just eaten much. The male, which had not fed for at least several hours, attempted to take the bone. However, the female snapped defensively at him and successfully retained the bone despite repeated attempts by the male over a 1-h period to steal it.

Even if the breeding female's active submission to her mate were really food-begging instead of subordination, one must still contend with the fact that sometimes the breeding female passively submits (Schenkel 1967) to the male. I observed this three times on Ellesmere (Table 1), but I never saw the breeding male passively submit to the female. Because passive submission seems to have nothing to do with food-begging, these observations seem to be clear evidence of subordination.

In attacks on prey, including both calf and adult musk-oxen, the breeding male and female appear to be equally involved, and they feed together side by side even though at times they keep yearlings away. Both breeders also hunt hares together, although on hunts that also involve yearlings, the breeding male seems more persistent than the female (Mech 1995*b*).

Both breeding male and breeding female scent-mark, and either can initiate double-marking (Haber 1977; Rothman and Mech 1979), depending on which is ahead during a particular moment of travel. For example, on 16 July 1993, during 4 km of travel, the Ellesmere Island breeding pair double-scent-marked three times; the male initiated two of them. Both male and female raise a hind leg during urine-marking, although the male raises his higher, possibly in keeping with his anatomy; both sometimes scratch the ground in association with marking.

During the early phases of pup care, the breeding pair shows a definite division of labor, with the female attending the den area and nursing the pups (Packard et al. 1992) and the male hunting away from the den and bringing food back to the female and the pups (Mech et al. 1999).

The male shows a strong imperative to relinquish food to the breeding female. For example, on 8 July 1992, when the Ellesmere male and female were equidistant from me in opposite directions, I threw the male an adult hare carcass weighing about 5 kg. The male grabbed it, but instantly the female rushed to him, snatched it from his mouth, and took it to the den. The male made no attempt to keep or regain the hare. I then gave the male a second hare of the same size. He ate the head and then took the rest of the carcass 0.5 km to the female and gave it to her. She cached it. Similar tests with smaller pieces yielded similar results.

Nevertheless, in keeping other pack members away from young pups, the breeding female seems to reign supreme, especially when the pups are less than 3 weeks old. In the Ellesmere Island pack, it was common for the breeding female to rush to the young pups whenever the breeding male or any other wolf began to approach them.

Furthermore, the breeding male defers posturally when he approaches the breeding female tending young pups. On 26 June 1990, I observed the breeding male walk toward the female in the den "excitedly wagging his tail and body." Similarly, on 18 May 1990 in Denali Park, Alaska, I observed radio-collared breeding male 251 in the Headquarters Pack (Mech et al. 1998) approach breeding female 307 when she was in a den with pups and begin to "wiggle walk," waving his back end and tail like a subordinate approaching a dominant. The female emerged from the den and the male then regurgitated to her. These were the only times I have ever seen a breeding male act submissively toward any other wolf, and it seems to indicate that the breeding female is temporarily dominant to even the breeding male before the pups emerge from the den.

The breeding female tends and protects the pups more than any other pack member. For example, mothers were the only pack members I ever saw picking up pups and carrying them. Furthermore, on one occasion I observed the breeding female of the Ellesmere Island pack being most aggressive against a muskox that once stood at the den entrance (L.D. Mech, see footnote 1). This agrees with Joslin's (1966) and Clark's (1971) observations. On the other hand, Murie (1944) reported that it was the breeding male which most aggressively chased grizzly bears (*Ursus arctos*) from around a den of pups.

Conclusions

The above observations show that, at least in summer, social interactions among wolf-pack members are not very different in intensity or quality from those among members of any other group of related individuals. Even the much-touted wolf dominance hierarchy is primarily a natural reflection of the age, sex, and reproductive structure of the group, with the breeding male dominating all others posturally and the breeding female garnering food from the male while she is tending young pups.

The typical wolf pack, then, should be viewed as a family with the adult parents guiding the activities of the group and sharing group leadership in a division-of-labor system in which the female predominates primarily in such activities as pup care and defense and the male primarily during foraging and food-provisioning and the travels associated with them (L.D. Mech, see footnote).

Dominance displays are uncommon except during competition for food. Then they allow parents to monopolize food and allocate it to their youngest offspring. Active submission appears to be primarily a food-begging gesture or a food-gathering motivator (Mech 1970). The role of active and passive submission in interactions between the breeding male and female when no offspring are present needs further exploration.

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