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Wolf Social Ecology

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THE FIRST REAL BEGINNING to our understanding of wolf social ecology came from wolf 2204 on 23 May 1972. State depredation control trapper Lawrence Waino, of Duluth, Minnesota, had caught this female wolf 112 km (67 mi) south of where L. D. Mech had radio-collared her in the Superior National Forest 2 years earlier. A young lone wolf, nomadic over 100 km² (40 mi²) during the 9 months Mech had been able to keep track of her, she had then disappeared until Waino caught her. From her nipples it was apparent that she had just been nursing pups.

“This was the puzzle piece I needed,” stated Mech. “I had already radio-tracked lone wolves long distances, and I had observed pack members splitting off and dispersing. My hunch was that the next step was for loners to find a new area and a mate, settle down, produce pups, and start their own pack. Wolf 2204 had done just that.”

During the decades since, we have seen this process many times, and it represents one of the primary ways in which wolves become breeders (Rothman and Mech 1979). However, there are several other ways, and it is only now, after 25 years of study and the wedding of wolf radio-tracking with biochemical analyses of wolf genetics (see Wayne and Vilà, chap. 8 in this volume), that we seem to have a reasonably complete picture of wolf social ecology (Meier et al. 1995; D. Smith et al. 1997; Mech et al. 1998).

Wolf Packs and Pairs: The Basic Social Units

The basic social unit of a wolf population is the mated pair. Known variations include a mature male and two

mature females; a mature male, his yearling son from a previous mating, and a new mate; and a mature female with a new mate and his younger brother (Mech and Nelson 1990b). There is no reason to believe that other similar combinations of a mated pair with various relatives of one or both members are not also possible.

There are two reports of packs of males, but these packs are not well documented or understood, and presumably are temporary until a mate is found. Ballard et al. (1987) reported without documentation that a pack of three males occupied a 3,077 km² (1,200 mi²) area of Alaska for over a year. Two radio-collared males split off from a Montana pack and lived together from June to September before being joined by a third animal of unknown age and sex (Ream et al. 1991).

The most unusual type of pack ever recorded formed in Yellowstone National Park 7 years after wolf reintroduction (D. W. Smith, unpublished data). During winter 2001–2002, three packs were formed of various assortments of at least twelve dispersers from four packs. Each new pack included a Druid Peak pack female born in 1997. Individuals moved among these packs, sometimes daily. By late spring, one pack contained two males from the Chief Joseph pack and four Druid Peak females. These wolves produced two litters in separate dens, merged in midsummer into six adults and four pups, and remained such at least into winter. Less is known about the other two new packs.

Mech also once recorded an adult male, his yearling son, and his three pups remaining together for 10 weeks after his mate (wolf 5091) was killed by other wolves (Rothman and Mech 1979). This situation can be

considered a temporary exception; a new mature female (5079) joined the pack after 10 weeks and remained with it, producing pups the next spring.

The natural extension of the mated wolf pair is the pair with its collection of offspring, or family, as earlier workers surmised (Olson 1938; Murie 1944; Young and Goldman 1944) and numerous radio-tracking studies have documented. In a thriving population, a wolf pair produces pups every year (Fritts and Mech 1981; Mech and Hertel 1983; Peterson, Woolington, and Bailey 1984; but cf. Mech 1995d). The offspring usually remain with their parents for 10–54 months, but except under special circumstances, all offspring disperse (Gese and Mech 1991; Mech et al. 1998). Packs therefore may include the offspring of as many as 4 years. A wolf pack, then, is some variation on a mated pair, and packs have contained as many as forty-two members, although most include far fewer (see table 1.1).

Adoptees

One poorly understood exception to the above basic rule is that strange wolves sometimes join packs already containing a breeding pair, at least temporarily (Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Messier 1985b; Ballard et al. 1987; Mech 1991b; Boyd et al. 1995; Meier et al. 1995). We will refer to these animals as “adoptees” (Meier et al. 1995) to distinguish them from wolves that enter a pack to replace a lost breeder (see below). Most adoptees are males, and most adoptions take place from February through May (Messier 1985b; Meier et al. 1995).

One of the main mysteries of this behavior is why strange wolves are sometimes allowed to join packs, whereas in so many other cases they are chased, attacked, or killed (Mech 1993a, 1994a; Mech et al. 1998). A clue may be the fact that most adoptees are 1–3 years old (Messier 1985b; Meier et al. 1995), whereas a high percentage of wolves killed by other wolves are adults (Mech 1994a; Mech et al. 1998). Tests with captive wolves confirm that degree of aggressiveness depends on the rank, age, and residency status of the wolves involved (Fox et al. 1974).

The incidence of packs adopting strange wolves would be very difficult to measure without sampling each wolf in every pack of a population and resampling over time. Based on genetic determinations, nine of twenty-seven packs from three study areas included ap-

parent adoptees (Lehman et al. 1992). However, most members of most packs were not sampled, and the sampling was done over several years. In an Alaskan population subject to harvesting by humans, over 21% of the wolves that dispersed over a 7-year period were accepted into other packs (Ballard et al. 1987). These diverse sampling schemes, plus the fact that adoptees remain in packs for periods of only a few days to over a year, preclude an estimate of the proportion of adoptees at any given moment. A rough guess might be 10–20%, and this proportion could well vary by time and place. (Additional information about adoptees can be found in the discussion of multiple breeding below.)

Pair Formation

As in the case of wolf 2204, described above, one of the main methods of pair formation is for dispersing wolves of the opposite sex to find each other. However, there are several other methods (“strategies”) of pair formation.

To understand the various breeding strategies wolves use, we must first make it clear that every wolf is a potential breeder, and as each begins to mature (see Kreeger, chap. 7 in this volume), its tendency will be to try to breed. This idea is contrary to earlier views that some wolves relinquish breeding “for the good of the species” (Rabb et al. 1967; Woolpy 1968; Mech 1970; Van Ballenberghe et al. 1975; Haber 1977).

Detailed studies of captive (Packard and Mech 1980; Packard et al. 1983, 1985) and wild wolves (Mech 1979a; Fritts and Mech 1981) show that many young wolves merely defer reproduction while still in their natal packs. In the basic social life of the wolf, this strategy can now be seen as merely a natural result of breeding competition, much like the failure to breed of many young male ungulates that lose in their competition with mature bulls.

The wolf population is comprised of tight, territorial social groups. To breed successfully, individual wolves must find a mate and a territory with sufficient food resources (Rothman and Mech 1979). In a saturated population, all territories are occupied, so the only local breeding possibilities will be to (1) wait until the established breeding position opens (A) in the natal pack or (B) in a neighboring pack, (2) become an extra breeder within the pack, (3) carve out a new territory from the established mosaic, or (4) usurp an active breeder.

Local Breeding Strategies

Wolves attempt all the above strategies and more. In Minnesota, a 2-year-old female bred with her stepfather after her mother was shot (Fritts and Mech 1981), illustrating strategy 1A above. The immigration of neighboring wolf 5079 into the pack described above after its breeding female (wolf 5091) was killed by other wolves illustrates strategy 1B; in this case, 5079 had produced pups in a neighboring pack the year before and apparently had lost them (L. D. Mech, unpublished data). Other cases of outside lone wolves joining existing packs to replace lost breeders have been documented by Fritts and Mech (1981), Mech and Hertel (1983), Peterson, Woolington, and Bailey (1984), and Stahler et al. (2002).

In some cases, wolves leave their pack but remain in the pack territory as "bidders," presumably waiting for a chance to breed (Packard and Mech 1980). Such wolves have solved one of the two parts of their breeding problem, finding a territory with resources. However, they may have to wait for a parent to perish before they can breed. Lindstrom (1986) believed that in red foxes, bidding might be the only type of breeding option for a weak individual.

Multiple Breeding

Rather than replacing a pack breeder, some maturing wolves breed in addition to the pack's established breeders while remaining in their natal pack. Such multiple breeding is favored by close genetic relatedness among the pack members (see below). Although some pertinent details about this behavior are still lacking, the behavior itself is well documented (Murie 1944; Rausch 1967; Clark 1971; Haber 1977; Harrington et al. 1982; Van Ballenberghe 1983b; Packard et al. 1983; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987; Meier et al. 1995). In no case was the relationship between or among the multiple-breeding females known, but one suspects that the breeding females were mother and daughter, because the known structure of wolf packs (see above) suggests that strange females are adopted into packs only rarely (Meier et al. 1995) unless the breeding female is lost (see above).

The important unanswered question when more than one female in a pack breeds is, which male bred the extra (nondominant) female? The likely suspect would be the dominant male, even if the extra female were his daughter, since close inbreeding is well known in captive

wolves (Medjo and Mech 1976; Packard et al. 1983; Laikre and Ryman 1991) and has long been considered common for wild wolves (Haber 1977; Woolpy and Eckstrand 1979; Theberge 1983; Shields 1983; Peterson, Woolington, and Bailey 1984). However, recent genetic studies of mated wolf pairs from the Superior National Forest (Minnesota) and Denali National Park (Alaska) populations indicated that inbred pairings were probably rare (D. Smith et al. 1997). This means chances are good that extra matings in a pack may be with immigrants from other packs, or even with outsiders through temporary liaisons. Or, if daughters of the dominant female breed, this could explain the role of adoptees (see above) and why most adoptees are males (Peterson, Woolington, and Bailey 1984; Messier 1985b; Meier et al. 1995).

Adoptee males may become interested in maturing females, which would explain their attraction to new packs. Sometimes such adoptees remain in their new pack from days (Peterson, Woolington, and Bailey 1984) to months (Fritts and Mech 1981) to over a year (Meier et al. 1995; M. E. McNay, personal communication). In Denali, an adoptee left his new pack after a year and was observed just outside the pack's territory with another wolf (a maturing female from the pack?); the adoptee and his mate produced pups in an adjacent territory the next year (Meier et al. 1995).

On the other hand, interest in a maturing female is not always an apparent motive for adoptees joining a pack, or for breeding pairs allowing them to do so. A male wolf radio-collared as a 10-month-old in Alaska during 1995 remained with his natal pack until June, then joined a breeding pair and their pups 58 km (36 mi) away in July, and remained with them at least through January and in their territory until the next July (M. E. McNay, personal communication). The pack had no maturing female when the adoptee joined, and when the pack's pups began maturing, the adoptee left.

Another situation in which multiple females in a pack could breed without inbreeding is when the father of maturing females is lost and replaced by a new male. This stepfather is then unrelated to any pack female and could breed any of them without inbreeding (Stahler et al. 2002).

For two reasons, it seems logical to suggest that multiple breeding is possible only when food supplies are flush (Mech et al. 1998), a hypothesis similar to the suggestion that multiple breeding is fostered by heavy exploitation (Ballard et al. 1987). First, ample food would

be required for more than one female to gain sufficient nutrition to produce pups; young pack members receive less food when it is scarce (Mech 1988a; Mech et al. 1998). Second, as will be discussed, maturing members are more likely to remain with the pack when food is more plentiful, whereas aggression increases when food is scarce.

Previous workers have emphasized the importance of social and behavioral factors in prompting dispersal (Haber 1977; Harrington et al. 1982). While these factors may be involved, we believe that nutrition stress underlies them, as social competition is very much a function of food abundance (see below).

Regardless of the uncertainties about various aspects of extra litters per pack, multiple breeding represents a viable strategy by which some wolves succeed in the breeding arena.

Budding and Splitting

Another breeding strategy is for a dispersed wolf and its new mate to try to set up a territory along the edges of its natal pack territory; this approach can involve either a male or a female from the natal pack. The animal frequents one end of the territory, presumably pairs with a floater (see below) or a similar member from a neighboring pack, and forms a territory adjacent to, or overlapping with, its natal territory, a process known as "budding" (Fritts and Mech 1981; Fuller 1989b; Meier et al. 1995; L. Boitani, unpublished data). Budding conforms to the territory inheritance hypothesis, which attempts to explain why group living in carnivores is a stable strategy (Lindstrom 1986).

A variation on this strategy is pack splitting. Pack splitting differs from budding in that, rather than a single wolf budding off a pack with a mate, a group of wolves splits off and assumes a new territory. Pack splitting in this sense is not the same as the temporary splitting of large packs during winter (Mech 1966b, 1970; Haber 1977; Carbyn et al. 1993). Rather, pack splitting as a form of budding is a permanent phenomenon.

Several cases of permanent pack splitting have been reported, all involving larger-than-average packs during or around the breeding season (Mech 1986; Meier et al. 1995; Hayes et al. 2000). In Denali, a pack of twenty split into two packs of eleven and nine and split the territory; at least one of the new packs produced pups that year (Meier et al. 1995; Mech et al. 1998). In one recolonizing population, packs split when they averaged twelve (± 1.5) wolves, and after 4 years of recolonization,

nine of twenty-eight (32%) packs were the products of pack splitting (Hayes and Harestad 2000a; Hayes et al. 2000).

It is probably when two related breeding pairs are present that packs split, perhaps after an immigrant male breeds a pack daughter. Presumably the additional members of the subunits are the previous offspring of each pair. Because breeders control the feeding of their offspring (see Packard, chap. 2 in this volume), they may compete too aggressively with other pack breeders as food needs peak in winter because of maximal pup weights. A solution that circumvents mortal competition among kin is to split the territory and resources (Mech 1970). This may be necessary only when food is scarce, thus explaining why large packs do not split every year.

Carving Out New Territories

Dispersers can also breed locally by carving new territories out of the existing pack territorial mosaic. Dispersers using such a strategy wander around the population ("floaters"), frequent areas along the interstices among territories (Mech and Frenzel 1971a; Rothman and Mech 1979; Fritts and Mech 1981; Meier et al. 1995), meet members of the opposite sex, mate, and attempt to set up a new territory (Rothman and Mech 1979). In some areas, however, such as parts of Quebec (Messier 1985b) and Denali (Mech et al. 1998), lone wolves do not seem to frequent pack territory edges and interstices. In any case, lone floaters may circulate over areas of 10,500 km² (4,100 mi²) or more, many times the size of local pack territories (Mech and Frenzel 1971a; Fritts and Mech 1981; Berg and Kuehn 1982; Merrill and Mech 2000; Wabakken et al. 2001).

Often loners frequent two or three areas along various pack territory edges and float long distances among them until they meet a mate in one of them; then they settle (Mech and Frenzel 1971a; L. D. Mech, unpublished data). In a recolonizing population in northwestern Minnesota, three floaters that were monitored for more than 4 months all paired, and at least two of the pairs produced pups; in the same population, seven of eight dispersers paired, usually within 20 days of dispersal (Fritts and Mech 1981). Although most lone wolves float independently, three pairs in this recolonizing population formed and then floated together, exploring areas until they found one to settle in (Fritts and Mech 1981). The only other area where this strategy seems to have been reported was Scandinavia (Wabakken et al. 2001).

Whether any of the pairs that attempt to carve out territories in an established population succeed depends in part on food abundance in the population. In the recolonizing population of northwestern Minnesota, these pairs tended to succeed (Fritts and Mech 1981), whereas 250 km eastward in the saturated, food-stressed Superior National Forest (SNF) population in the early 1970s (Mech 1977b), they tended to fail (L. D. Mech, unpublished data).

In the SNF during 1969–1989, a time that included periods both of food stress and of improved conditions, 65% of those wolves that dispersed as adults, 26% as yearlings, and 8% as pups succeeded in pairing and denning (Gese and Mech 1991). In an increasing wolf population in Denali National Park during 1986–1991, nine (56%) of sixteen new pairs succeeded in founding new packs that lasted a year or more (Meier et al. 1995).

Usurping a Breeder

A last way in which maturing wolves can breed in their own population is to usurp an established breeding position. An example of this approach was seen in the SNF, where a 3-year-old female bred with her stepfather a year after her mother bred with him and left (Mech and Hertel 1983); whether the mother was ousted or left voluntarily is unknown. On Ellesmere Island, a 3-year-old daughter took her mother's breeding role while the mother remained in the pack as a helper (Mech 1995d). In this case, the male had been the mother's mate for 2 years; he could have been the daughter's older sibling or an unrelated wolf, but probably was not the daughter's father.

No doubt the most dangerous strategy for gaining a breeding position would be to challenge an established breeder. Such challenges have been observed in captive situations, where yearling sons challenged their fathers and bred with their mothers (Zimen 1976; Packard et al. 1985). However, such fights that could become mortal in captivity might never take place in a wild pack, where a beaten contender can escape; furthermore, the best evidence so far is that close inbreeding does not occur where outbreeding is possible (D. Smith et al. 1997).

Nevertheless, wolves do often fight to the death in the wild (see below), and the losers are usually wolves encountered near a territory edge or inside a neighbor's territory (Mech 1994a; Mech et al. 1998). A disproportionate number of the dead wolves are adult breeders, but subordinate, maturing animals are also killed. There is a strong possibility that some of these fights result

from potential breeders challenging established breeders. The best such record was Messier's (1985b) observation in Quebec that a presumed breeding male was killed one March at the time his pack adopted a young immigrant male.

An incident that L. D. Mech (unpublished data) observed in the SNF during the breeding season (Mech and Knick 1978) also suggests such a challenge. The SNF Greenstone pack (four members) trespassed south of its southern neighbor, the Pagami Lake pack (five members), on 15 February 1972, then returned to its territory. The next day, Mech watched as the Greenstone pack entered the Pagami pack's territory from the south and attacked the sleeping five. At least one wolf from the Pagami pack was wounded, and the Greenstone pack returned to its territory. The only radio-collared Pagami wolf was alone the next eight times it was seen during the next month, and then dispersed. The one radio-collared Greenstone wolf was not seen with more than two others during the next twelve observations through 13 March; then her signal was lost. By fall, however, a newly radio-collared pup was part of a pack of six living in the former territories of both packs. Did the neighboring breeders form one pair after the fight, oust the others, and usurp both territories?

In Denali, the McKinley River pack (ten members) invaded the territory of the Bearpaw pack (also ten members) and, between January and March 1988, killed all three radio-collared members of the Bearpaw pack, wounded at least one other member, and may have killed two others (Meier et al. 1995). Two McKinley River wolves and two new wolves (former Bearpaw members?) then usurped the Bearpaw pack territory, even using the Bearpaw pack den.

Distant Dispersal

Besides the several strategies described above for obtaining a breeding position in the local population, wolves also use a strategy that takes them into a new population or to the very edge of the species' range. This strategy, called directional dispersal (Mech and Frenzel 1971a; Mech 1987a), is a tendency to move a long distance in more or less a single direction. Wolves of both sexes have dispersed to areas up to 886 km (531 mi) away (Fritts 1983; Ballard et al. 1987; Boyd et al. 1995), and some have crossed four-lane highways and open areas and circumvented large lakes and cities (Mech, Fritts, and Wagner 1995; Merrill and Mech 2000; Wabakken et al. 2001; L. Boitani, unpublished data). When long-distance

dispersers settle, they may attempt to squeeze into the territorial mosaic of a distant population, join an existing pack, or pair with a member of the opposite sex in an area uninhabited by breeding wolves (Rothman and Mech 1979; Fritts and Mech 1981; Berg and Kuehn 1982; Peterson, Woolington, and Bailey 1984; Messier 1985b; Ballard et al. 1987; Fuller 1989b; Meier et al. 1995; L. D. Mech, unpublished data).

Frequency of Various Strategies

The relative proportions of potential breeders that use these various breeding strategies have not been measured (but see below). Those proportions must vary over space and time and depend a great deal on food supply and whether the population is increasing, decreasing, or stable (see Fuller et al., chap. 6 in this volume). However, a general idea of those proportions can be obtained from the proportions of wolves of various ages that disperse and the distances they move. Near-dispersers would include those wolves that attempt to breed with neighbors through biding, budding, or replacing established breeders. Distant-dispersers would be those that chance finding or founding new populations.

Some information on proportions of breeding strategies can be gleaned from both the SNF and Denali studies. In the SNF population, which between 1969 and 1989 declined, stabilized at a low level, and then increased, the pairing success of some seventy-five wolves that dispersed from their packs was examined (Gese and Mech 1991). A significantly greater proportion of maturing animals dispersed during the declining and increasing phases than during the stable phase, probably reflecting the least competition during the stable phase. Most of the wolves dispersing at less than 1 year of age traveled more than four territories away, whereas most yearlings and adults remained within a radius of three territories. (More details about dispersal are presented below.)

In the increasing Denali population, sixteen new pairs formed in 1986–1991 (Meier et al. 1995). Two of these pairs died out without producing pups; five produced pups, but failed to hold their territory beyond a year, in most cases because the adults were killed by other wolves; and nine produced pups and held territories for a year or more. Of the nine successful pairs, it is significant that at least seven succeeded through “budding,” or carving out a territory partly inside or just adjacent to their natal territory.

The Breeding Flux

Competing with maturing wolves for new breeding positions are lone adults that have left or lost their mates or breeding positions. Individuals such as wolf 5079 in the SNF, mentioned above, as well as examples recorded by Fritts and Mech (1981), Peterson, Woolington, and Bailey (1984), Mech (1987a), L. D. Mech (unpublished data), Ream et al. (1991), and Meier et al. (1995), indicate that many adults join the floating members of the wolf population to compete with the maturing members. These adults tend to remain within 50 km of the area they leave, at least in Minnesota (Gese and Mech 1991).

Given all the above breeding strategies, a wolf population can be viewed as a highly dynamic system in which breeding pairs hold territories and pump out numerous offspring that travel about, criss-crossing the population and striving to gain their own breeding positions. In this flux, each pack tries to hold its position while competing with neighbors that try to expand their territories (see below) as well as with new breeding pairs, local lone wolves, and immigrants that are all trying to leverage themselves into the population structure.

The flexibility in the sizes of wolf packs and territories helps buffer the constant fluctuations in social and ecological factors that wolves face. Wolf populations are constantly churning, and a high proportion of their members are temporary. In the Denali National Park population, which is one of the least human-disturbed wolf populations anywhere, only 15% of wolves under 3 years of age remained in the population for more than 5 years (Mech et al. 1998). Thus at least some of the population's long-term breeders must be immigrants, another indication of the constant genetic mixing of the population.

Why Do Wolves Live in Packs?

The wolf and the wolf pack are as closely linked in the human mind as a child is linked to a family, and rightly so. The human family is a good analogy for the wolf pack. The basic pack consists of a breeding pair and its offspring, which function in a tight-knit unit year-round. As with humans, male wolves generally are larger than their mates, about 20% heavier in general (Mech 1970).

The offspring of the breeding pair often include members of more than one litter. Wolf pups reach adult

size by winter, so the presence of pups then gives the pack the appearance of a group of adults. Because at least some young often remain with the pack for a year or more, when new pups are born, the social group constantly appears to contain more than a pair of adults.

Why do wolves remain with their parents for as much as 10–54 months while many other mammals leave sooner? At least some wolf pups can survive without their parents when as young as 4 months of age (Fritts et al. 1984, 1985). Their permanent canine teeth are in place by 7 months (Van Ballenberghe and Mech 1975), their long bones cease growth by 12 months (Rausch 1967), and at least some males and females are capable of breeding at 10 months (Medjo and Mech 1976).

The Pack as Nursery

One answer might be that there is great variation in wolf maturation. Some wolves are not reproductively capable even at 3 years of age (Mech and Seal 1987). Physiologically, wolves may not be completely “mature” until about 5 years of age. U. S. Seal et al. (unpublished data) found that wolf androgen and estrogen levels increased until this age. Thus the continued association of young wolves with their natal pack may simply be a way for the young to mature while still being subsidized by their parents. From the parents’ standpoint, caring for young until they are mature may be the best way to ensure their original investment. In addition, long association with parents would increase the opportunity for offspring to learn the more subtle components of hunting and foraging behavior that are not innate (Leyhausen 1965, cited in Eaton 1970).

Pack Size and Prey Size

On the other hand, there is some evidence that wolf pack sizes may be influenced by other factors. There has been much theoretical discussion of carnivore group sizes (Murie 1944; Mech 1970; Kleiman and Eisenberg 1973; Zimen 1976; Bekoff and Wells 1980; Rodman 1981; Bowen 1981; Lamprecht 1981; Brown 1982; D. W. Macdonald 1983; Packer and Ruttan 1988; and others). The theory holds that pack size should vary with prey size up to some optimum number; this optimum should be that which allows predation with the least energy expenditure and the most energy return (D. W. Macdonald 1983).

Wolf pack sizes tend to be largest where wolves prey on the largest ungulates. Despite records of hundreds of wolf packs from many areas, however, the relationship of pack size to prey size is not definitive (see Fuller et al., chap. 6 in this volume). This is partly because of the extreme variation in pack size within each area and because in many of the areas studied the wolves were subject to harvesting or control.

Pack size data are available for relatively unexploited wolf populations in Minnesota, Denali National Park, Alaska, Wood Buffalo National Park, Alberta, and Yellowstone National Park. Other data from exploited populations tend to support these data, but are less definitive because of the possible effect of exploitation. The smallest packs tend to feed on garbage and small animals, and the largest on moose and bison (table 1.1).

However, this pattern is only a very general tendency (Mech 1970). For example, in 1971–1991, the mean pack size for Isle Royale, in Lake Superior, Michigan, where moose are the only ungulate prey, was 7.5, whereas for north-central Minnesota, where white-tailed deer were the exclusive prey, pack size averaged 7.3 (see table 1.1). Average pack sizes for wolves feeding on deer and moose are significantly smaller than for those feeding on elk and caribou (see Fuller et al., chap. 6 in this volume). Nevertheless, the largest packs where moose and bison were preyed on were twice as large as the largest packs from deer areas (see table 1.1).

Complicating Factors

As discussed above, it is reasonable to try linking group size to prey size. Some of the earliest wolf biologists assumed that wolf packs exist because they may promote greater hunting efficiency (Murie 1944), and this conclusion seems logical (Mech 1966b, 1970; Zimen 1976; Peterson 1977; Nudds 1978; Carbyn et al. 1993). Several important factors, however, complicate the picture.

If large numbers of wolves were necessary to prey on large ungulates, it would be difficult for lone wolves and pairs to survive and produce the offspring that enlarge the pack. In fact, large numbers of wolves are not necessary to kill large prey. Single wolves have been recorded to kill even the largest of the wolf’s major prey species, including adult moose (Cowan 1947; A. Bjärvall and E. Isakson, personal communication; Thurber and Peterson 1993; Mech et al. 1998), muskox (Gray 1970), and bison (D. Dragon, cited in Carbyn et al. 1993).

TABLE 1.1. Distributions of wolf pack sizes primarily from unexploited populations using prey of different sizes

Main prey	Pack size																	\bar{x}^b	Largest ^c	Source
	N ^a	2	3	4	5	6	7	8	9	10	11	12	13	14	15	>15				
White-tailed deer	78	21	7	9	13	10	6	2	6	2	—	1	—	—	1	—	4.9	(17)	Mech 1986	
White-tailed deer	35	3	1	2	2	6	6	2	6	2	2	2	1	—	—	—	7.3	(13)	Fuller 1989b	
Moose	48	3	6	2	7	10	3	4	7	1	1	2	1	1	—	—	6.6	14	Mech 1986	
Moose	50	7	4	4	3	3	6	5	1	5	4	1	2	2	—	3	7.5	18(22)	Thurber and Peterson 1993	
Moose/caribou	106	8	6	4	9	7	13	13	7	8	4	8	2	1	4	12	9.1	29	Mech et al. 1998	
Bison ^d	206																9.4	(42) ^e	Carbyn et al. 1993	
Garbage, etc. ^f	24	12	2	2	3	2	3	—	—	—	—	—	—	—	—	—	3.6	(7)	Boitani and Zimen 1979	
Garbage, small animals ^f	21	6	7	4	2	1	1	—	—	—	—	—	—	—	—	—	3.4	7	Mendelssohn 1982	

^aPack-years, so many packs are represented during several years.

^bWeighted.

^cNumbers in parenthesis indicate pack sizes not reported as part of distribution of pack sizes but rather reported independently.

^dLight to moderate exploitation.

^eFau and Tempny 1976; cited in Carbyn et al. 1993.

^fExploited population.

Even when a wolf pack attacks prey, not every pack member contributes significantly to the attack. Because of the general assertiveness and experience of the breeding pair, they tend to take the lead in chasing and attacking prey, and it is unclear how much the younger pack members contribute (see Mech and Peterson, chap. 5 in this volume). In a pack consisting of a breeding pair and their 7-month-old pups hunting for the first time, for example, it seems unlikely that the pups would assist very significantly in the kill.

Another factor that few workers have considered is that wolf pack size in the usual sense is not necessarily the same as hunting group size. Most pack size observations are made in winter, when the pack is nomadic. Thus the adults usually bring the whole family with them when they hunt. In summer, however, the den is the social center, and adults radiate out from it in foraging groups of various size (Murie 1944; Mech 1970, 1988a; Ballard, Ayres, Gardner, and Foster 1991). Even in winter, wolf packs do not always hunt at full size, especially when they are large. Most packs vary in the numbers traveling together throughout the winter (Stenlund 1955; Mech and Frenzel 1971a), as various members lag behind during travels, some visit old kills, or others disperse temporarily (see below).

In addition, packs sometimes split temporarily (but for days at a time) into smaller hunting groups, similar to the way African lion prides split (Packer et al. 1990). A pack of fifteen wolves on Isle Royale split into two groups about half the time during the 1961 winter study (Mech 1966b), and split again in 1963 and 1965 (Jordan et al. 1967). Similar pack splitting during winter has also been reported for Denali (Haber 1977), Italy (Boitani and Zimen 1979), and Wood Buffalo National Park (Carbyn et al. 1993). Therefore, published pack sizes, which are almost always stated as the maximum number of wolves observed over winter, are not necessarily hunting group sizes, thus complicating any analyses that do not consider this.

Pack Size and Hunting Efficiency

It certainly seems reasonable that, at least to some extent, hunting in groups would increase hunting efficiency even if no cooperative strategy were used. Multiple hunters, even if inept or inexperienced, would seem to yield greater sensing, chasing, restricting, attacking, and killing power than single hunters.

However, possibly offsetting this advantage is the fact that multiple hunters must also share the proceeds (Brown 1982). This and numerous other theoretical and empirical considerations have led some workers to the conclusion that “cooperative hunting is more often a consequence of gregariousness than its evolutionary cause” (Packer and Rutan 1988, 189).

A good test of the hypothesis that larger groups of wolves are more efficient at hunting or killing prey is to determine amount of food obtained per wolf for packs of various sizes. On Isle Royale during 1959–1961, the pack of about fifteen wolves mentioned above preyed on moose, but in 1961, when this pack split into two about half the time, the amount of food obtained was greater than during the previous 2 years, when the pack hunted as a unit (Mech 1966b). Similarly, lone wolves in Minnesota killed more prey per wolf than a pack of five (Mech and Frenzel 1971a), and pairs killed more prey per wolf than packs (Fritts and Mech 1981; Ballard et al. 1987, 1997; Thurber and Peterson 1993; Hayes et al. 2000).

When this hypothesis was tested more rigorously with wolves and moose on Isle Royale, the result was the same: the larger the pack, the less food obtained per wolf (fig. 1.1). Synthesizing data from many studies including most wolf prey gave the same result (Schmidt and Mech 1997).

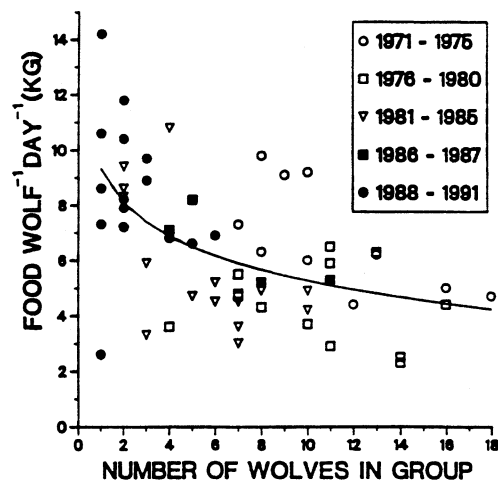


FIGURE 1.1. Food availability (kg/wolf/day) for different group sizes of gray wolves preying on moose in Isle Royale National Park during winter, 1971–1991 ($Y = 9.31 - 1.76 \log_{10} X$). (From Thurber and Peterson 1993.)

Sharing the Surplus

What other factors might cause wolves (or other carnivores) to live in groups, then? And why do the largest packs seem to be those preying on the largest quarry? Put another way, why don't all young wolves disperse from their natal pack as soon as they are fully developed, at about 7–12 months?

It turns out that they do, at least in some areas, and these cases are instructive. During the early 1970s in Italy, when few ungulates were present, most packs consisted of little more than pairs in winter (see table 1.1). Similarly, packs are small in Israel, where wolves feed extensively on garbage and small animals (Mendelssohn 1982). That both the Italian and Israeli wolves were also subject to human exploitation confounds attempts to definitively relate small pack size to small scattered food sources, but the data are suggestive. With coyotes, pack size does relate to food source size (Bowen 1978).

If wolf pack size is related to food source size, but increased pack size does not necessarily yield greater hunting efficiency, then why live in packs? The answer seems to be that the evolution of grouping in wolves has facilitated subsidy of young wolves by their parents through the sharing of large prey (Mech 1970, 1991b; Schmidt and Mech 1997). Since adults prey on large animals, a surplus of food suddenly becomes available periodically. Making this surplus available to kin is the most efficient approach adult wolves can take, except for eating it and caching it. Without a sufficient number of feeders, this surplus can be lost to competitors, scavengers, insects, and bacteria. Ravens can remove up to 37 kg (17 pounds) of a carcass per day, and can usurp some 66% of a lone wolf's kill, compared with only 10% of the kills of a pack of ten (Promberger 1993; see also Stahler 2000).

The kin selection explanation of why wolves live in packs (Schmidt and Mech 1997) fits the resource dispersion hypothesis. This theory holds that food quantity and distribution is the primary cause and determinant of group size (D. W. Macdonald 1983; von Schantz 1984). The types of prey wolves rely on have unique characteristics of richness (a large amount of food per prey), renewal (slow turnover), and heterogeneity (highly patchy distribution and low density), which are the key conditions that the hypothesis predicts would foster group living (D. W. Macdonald 1983).

Wolf parents allow their young to remain with them so long as their food supply can support more individuals than themselves. From the offspring's standpoint, if

the food supply is secure, it is advantageous for them to stay with their parents rather than trying to find resources on their own, at least until the urge to breed compels them to seek a mate outside the natal pack. Although there are no experimental results confirming this theory, the fact that pack size tends to correlate with food supply (Mech 1977a; Messier 1985a) lends support to the theory.

Clearly wolf packs that prey on smaller animals such as deer would have less surplus food available per kill than packs that prey on moose or bison. Packs preying on moose or bison could afford to include a larger number of offspring, thus improving the inclusive fitness of the family (Rodman 1981). An efficient pair of adult breeders in a moose area, then, could feed members of two or three of their last litters of offspring. This would enhance the survival of those offspring and increase the chances of the parents' own genes being disseminated. Inclusion of these maturing wolves on hunting forays would also give them practice and experience in hunting.

If maturing wolves accompany their parents in packs to gain easy forage, this may explain why large packs are not necessary to take large prey, yet the largest packs are usually found in areas with the largest prey. Simply put, large prey allow large packs, but do not require them.

When Mech (1966b) watched a pack of fifteen wolves lined up to feed around a moose carcass, he was impressed with the fact that not many more could have fit around it. Had there been any more wolves, some would have to have gone hungry. Long before, Adolph Murie (1944) had suggested that prey size might limit pack size in this way.

Such a relationship could also explain why large packs are occasionally found temporarily even among wolves hunting smaller prey. If enough smaller prey could be killed either concurrently or in close sequence, more individuals could accompany a wolf pack than otherwise. During 1990, when the East Fork pack in Denali numbered up to twenty-nine, they often killed more than one sheep or caribou at a time (Mech et al. 1998). This behavior conforms to the theory that when feeding constraints are relaxed, hunting group size should increase (Caraco and Wolf 1975).

Pack Size Regulation

Besides the general factors discussed above that affect pack size, other specific factors are also important. If the reason young wolves stay with their natal pack is to use their parents' provisioning skills to maximize their food intake during growth and maturation, this strategy would also explain certain aspects of dispersal. As indicated above, wolves mature at varying rates, probably because of varying nutrition. Thus it would be adaptive for them to do whatever possible to maximize their food intake. Because their parents have nurtured them throughout their lives, their tendency probably would be to remain with their parents until something forces them away.

However, because there are usually new offspring annually, with a greater need for parental nurturing, as the previous litters age, they must begin to compete with younger siblings for food. The parents' priority is to feed the youngest offspring; if there is enough to go around, then the older offspring are allowed to feed (L. D. Mech, unpublished data). (In the rare year when there are no pups, the adults continue to provision the yearlings, as would be expected [Mech 1995c,d].)

Some wolves disperse when as young as 5 months of age (Fuller 1989b), whereas others may remain with the pack for up to 3 years (Gese and Mech 1991), or occasionally longer (Ballard et al. 1997). As will be discussed below, intense food competition may be one of the main triggers for dispersal. If so, then perhaps when food is scarce, adults stop provisioning young as early as 5 months of age. By then, the young would be physically able to survive on their own (see above). This also would be a time when the adults would have to maximize their own intake to prepare for the next litter of pups.

It is probably only when food is sufficient that adults share it with their older offspring, and those offspring might then remain with the pack. Such offspring even provision the new litter of pups at the den, although they also sometimes usurp the pups' food as well (see Packard, chap. 2 in this volume).

Thus food competition could be the feedback mechanism that regulates pack size through dispersal. Prey size, and at times prey abundance, would set the upper limit to the number of individuals that could share without undue competition; any excess would disperse. If food were sparse, the young would disperse earlier; if abundant, they would remain longer, ideally until they were sexually mature. At that point, sexual competition

and aggression might be the factor triggering dispersal.

A finer adjustment factor to this system could involve the pack dominance hierarchy (see Packard, chap. 2 in this volume). Presumably, as food competition increases, it is not only the lower-ranking classes of pack members (e.g., yearlings) (Messier 1985b) that must leave, but also the lower-ranking members within a class. Food competition has long been seen as a factor affecting the lowest-ranking pack members most adversely (Zimen 1976). In coyotes, it is also the most subordinate individuals that have least access to pack food resources and leave the pack soonest (Bekoff 1977b; Gese 1995).

This system of determining wolf pack size would explain why the age of offspring dispersal is so variable (Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987, 1997; Mech 1987a; Potvin 1988; Gese and Mech 1991) and why that age varies from year to year, with entire litters remaining with a pack in some years or dispersing in others (Mech 1995d).

The best evidence that food competition does affect dispersal comes from southwestern Quebec. There, yearling and "adult" wolves (which could have been as young as 2 years old) in an area of low moose density made significantly more excursions of 5 km (3 mi) or more from their territories than did yearlings and adults in a nearby area of high moose density; furthermore, more females than males made such excursions (Messier 1985b). These excursions lasted from a few days to a few months, averaged more than 22 km (13 mi) in straight-line distance, and eventually culminated in dispersal. On Isle Royale, more wolves also left packs during periods of lower food supply (Peterson and Page 1988).

Dispersal

As indicated above, most wolves disperse from their natal packs. Unless it assumes a breeding position within the pack, which is rare, any wolf born into a pack will leave it. In fact, each wolf pack can be viewed as a "dispersal pump" that converts prey into young wolves and spews them far and wide over the landscape. On the average, then, a thriving pack of three to nine members producing six pups each year (see Fuller et al., chap. 6 in this volume) thus "pumps out" about half its members annually.

In some circumstances, dispersal is more like a pulsating of members back and forth from the pack, for members may leave temporarily (see above) and return one to six times before finally dispersing (Fritts and

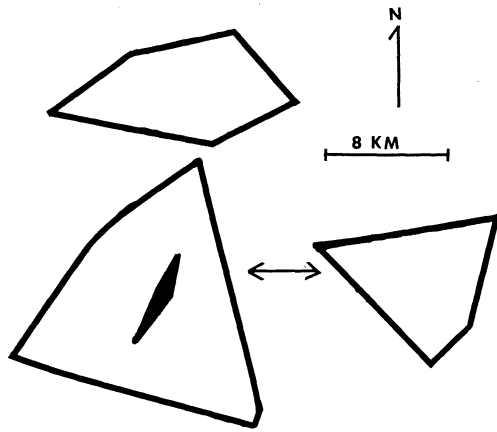


FIGURE 1.2. Territories of female wolf 6433 in the Superior National Forest of Minnesota. Upper polygon, 6433's natal territory; lower polygons, territories between which 6433 and her mate alternated from 11 January 1984 through 11 June 1984, after which they broke up and 6433 returned to her natal territory; blackened area, where the pair localized 5–29 April 1984.

Mech 1981; Van Ballenberghe 1983a; Peterson, Woolington, and Bailey 1984; Messier 1985b; Ballard et al. 1987; Mech 1987a; Potvin 1988; Fuller 1989b; Gese and Mech 1991). On the other hand, some wolves disperse without any known preliminary forays (Mech 1987a; Boyd et al. 1995; Mech et al. 1998; L. D. Mech, unpublished data).

Extraterritorial forays by wolves can even involve pairing, territorial establishment, and localizing during the denning season, followed by a return to the natal pack half a year later (Mech 1987a; Mech and Seal 1987) (fig. 1.2). In fact, wolf dispersal is probably most accurately viewed as a continuum, from single, short departures from the natal pack through intermittent and multiple extended forays to permanent, distant emigration. These movements appear to be motivated by attempts to maximize food input and opportunities to breed. However, they may also be underlain by a predisposition in some individuals to travel long distances, as we will see below.

Although predispersal forays might be viewed as “trial” or “exploratory” dispersals, they might also be merely movements that internal state plus food supply and social circumstances force on young wolves, and might not have any trial or exploratory function. Data from red foxes, however, tend to support the exploratory nature of some predispersal movements. Predispersing foxes moved much faster and spent little time resting or foraging during exploratory trips (Woollard and Harris 1990).

Sex and Age of Dispersers

Wolves of both sexes disperse, and there seem to be few consistent male-female differences in dispersal characteristics. In some regions or times, males apparently disperse farther or at a higher rate (Pulliainen 1965; Peterson, Woolington, and Bailey 1984; Wabakken et al. 2001). However, at other times or places females disperse farther on average, even though the longest-distance dispersers were males (Fritts 1983; Ballard et al. 1987). Nevertheless, the record dispersal lengths of males and females tend to be about the same (see below).

In south-central Alaska, males dispersed at a higher rate than females (Ballard et al. 1987). Perhaps such a difference has some ecological significance, because males showed the same propensity on Alaska's Kenai Peninsula during 1976–1980, whereas during 1980–1981, female dispersal tended to balance out the sex ratio of dispersers (Peterson, Woolington, and Bailey 1984). In southwestern Quebec, female pre-dispersers spent more time away from their packs than did males (Messier 1985b).

As already discussed, wolves disperse from their natal packs at a wide variety of ages, and this variation is probably related to food competition within individual packs. Wolves as young as 5 months and as old as 5 years have dispersed from natal packs, but the commonest age of dispersal in many areas is 11–24 months (Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Messier 1985b; Ballard et al. 1987, 1997; Mech 1987a; Potvin 1988; Fuller 1989b; Gese and Mech 1991; Hayes and Harestad 2000a; Mech et al. 1998). Older adults that disperse from packs are often individuals that had immigrated into those packs (Meier et al. 1995; L. D. Mech, unpublished data). Fritts and Mech (1981) and Boyd et al. (1995) suggested that high rates of yearling dispersal were related to a high potential for colonization in the immediate area, but Gese and Mech (1991) found the same rate of yearling dispersal in a saturated population (63% of dispersers) as in the populations discussed by Boyd et al. 1995).

Notable exceptions to the usually high rate of yearling dispersal were reported under two conditions. In northwestern Alaska's exploited population, the average age of dispersal was about 3 years (Ballard et al. 1997). In the reintroduced Yellowstone population (see Boitani, chap. 13 in this volume), the mean age of the thirty wolves that had dispersed by October 2001 was 2 years and 1 month, with a range of 1 year and

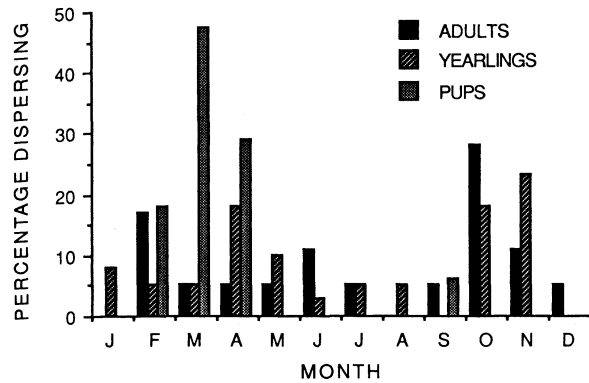


FIGURE 1.3. Month of dispersal for three age classes of dispersing wolves in the Superior National Forest, Minnesota, population, 1969–1989. (From Gese and Mech 1991.)

5 months to 3 years and 7 months (D. W. Smith, personal communication).

Dispersal Season and Triggering Mechanisms

The fact that wolves disperse primarily while beginning to mature sexually tends to implicate reproductive development (puberty) as a factor helping to trigger dispersal, or at least necessary for it. Such is the case with many other species (Howard 1960).

Although wolves have dispersed at every time of year, those in most areas leave during autumn and early winter or around the spring denning season (fig. 1.3). Most of the studies cited above agree with this conclusion, although not those in northwestern Alaska (Ballard et al. 1997). Pups that disperse in their first year usually leave from January to May (Fuller 1989b; Gese and Mech 1991).

The spring and fall peaking of dispersal in most areas suggests that one of the triggers for dispersal is social competition. During spring, aggression related to breeding is maximized (Rabb et al. 1967; Zimen 1976), and adults are presumably building reproductive fat stores. In fall, pups begin traveling with the adults and become nomadic with the pack. Their food needs peak at this time (Mech 1970), yet the pups are still dependent on the adults, so food competition also begins to peak.

Because food availability is variable throughout the year, dispersal could be expected during any season, but should peak when food and social competition peak. In Quebec, more yearling and adult wolves dispersed from packs living on a low prey base than from nearby packs

living on a high prey base (Messier 1985b). When food stress increased on Isle Royale, so did dispersal rate, and dispersal rate was inversely related to pack size (Peterson and Page 1988). Furthermore, more dispersed lone wolves were present there during periods of low prey availability (Thurber and Peterson 1993).

In the Yukon, wolves repopulating an area from which wolves had been extirpated dispersed at increasing rates each year, and dispersal rates were positively correlated with pack size and negatively correlated with the ungulate biomass/wolf ratio (Hayes and Harestad 2000a). The larger the packs, the more competition and potential dispersers there are, and the greater the biomass of prey available, the less competition. The relatively high amount of food available to wolves in northwestern Alaska (Ballard et al. 1997), as well as to those in Yellowstone National Park (Mech et al. 2001), probably explains the high age of wolf dispersal in those areas (D. W. Smith, personal communication).

Thus competition and aggression, usually centered on food, can be considered a primary trigger for wolf dispersal. Postulating that aggression fostered by food and breeding competition helps trigger dispersal may seem to contrast with Bekoff's (1977b) view of the role of aggression in dispersal. However, Bekoff believed that aggression was not the "immediate cause" of dispersal, meaning that dispersers do not seem to be actively chased away. He did stress that avoidance of social interactions was characteristic of several species just prior to dispersal.

Bekoff's emphasis on social avoidance in dispersers accords with findings in both red foxes (Harris and White 1992) and coyotes (Gese 1995) that dispersers associate less with their social groups than do nondispersers. This lack of sociality, however, does not necessarily rule out aggression as a factor. In all the above situations, the aggression could merely be covert, or at least less perceptible, to a human observer. Schenkel (1947) emphasized that just the fixed stare of a dominant wolf wields great power over the behavior of subordinates.

In any case, wolves are often aggressive toward low-ranking wolves (Mech 1966b; Jordan et al. 1967), including their relatives, at least in captivity (Rabb et al. 1967; Packard et al. 1983). Thus chances are good that overt aggression, at least during some seasons, and possibly covert aggression at other times, is a strong factor in wolf dispersal (Zimen 1976).

TABLE 1.2. Frequency of wolves dispersing alone and with associates

Area	N	Alone	With 1	With 2	With > 2	Reference
Minnesota	9	9	—	—	—	Fritts and Mech 1981
Minnesota	28	23	1	1	—	Fuller 1989b
Minnesota	75	75	—	—	—	Gese and Mech 1991
Minnesota	7	7	—	—	—	Berg and Kuehn 1982
Alaska	21	15	3	—	—	Peterson, Woolington, and Bailey 1984
Quebec	11	7	2	—	—	Messier 1985b
Quebec	15	15 ^a	—	—	—	Potvin 1988
Alaska	38	? ^a	1	? ^a	? ^a	Ballard et al. 1987
Wisconsin	16	16	—	—	—	Wydeven et al. 1995
Montana	13	11 ^a	1 ^b	—	—	Boyd et al. 1995

Note: The figures given here are probably minimum numbers because often it is not known whether a dispersing wolf has associates.

^aNot explicitly stated.

^bMentioned by Ream et al. (1991) for same study as Boyd et al. (1995).

An intriguing piece of information that seems to contrast with the food competition theory of dispersal is the observation in northwestern Alaska that the highest annual dispersal rate was found following a rabies epizootic (Ballard et al. 1997). However, as the authors of the study indicated, this high dispersal rate may have been due to the resulting breakup of pack structure.

Individual versus Group Dispersal

Most wolves disperse alone, but there are notable exceptions, although little is known about such group dispersal (table 1.2). Among twenty-one wolves recorded dispersing from the Kenai Peninsula, in three cases, the animals dispersed as duos, but then split (Peterson, Woolington, and Bailey 1984). Seven of nine dispersers in Quebec dispersed alone (Messier 1985b), and in north-central Minnesota, one trio of wolves and one pair dispersed, whereas twenty-three other wolves dispersed alone (Fuller 1989b). Wolves also dispersed or made long forays in dyads in northern Montana (Boyd et al. 1995), and in Alaska, an adult female and five pups traveled some 72 km (43 mi) out of their territory in August (Ballard et al. 1997).

When groups of wolves permanently leave an area, their movements may not really be dispersal, which is defined as movement from a natal to a breeding site (Bekoff 1977b). Rather, the wolves may be emigrating. The most unusual group emigration reported was that of the Little Bear pack of eleven wolves, which moved 250 km (150 mi) from their territory in Denali National Park (Mech et al. 1998) (see below).

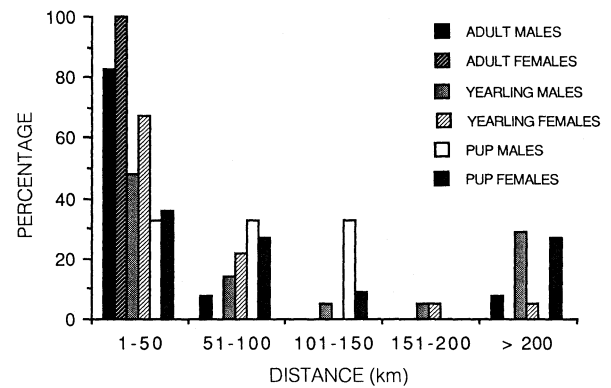


FIGURE 1.4. Distance traveled by three age classes of dispersing wolves in the Superior National Forest, Minnesota, population, 1969–1989. (From Gese and Mech 1991.)

Dispersal Distances

The distances wolves disperse reflect the great variation in types of dispersal, from merely moving to an adjacent territory through floating around the local population to dispersal up to 886 km (532 mi) distant (Mech and Frenzel 1971a; Van Camp and Gluckie 1979; Fritts and Mech 1981; Fritts 1983; Mech 1987a; Ballard et al. 1983; Messier 1985b; Gese and Mech 1991; Wabakken et al. 2001). The data suggest that the younger the disperser, the farther it disperses (fig. 1.4; see also Wydeven et al. 1995). This relationship might relate to the growing familiarity with the area or with the local population gained by a wolf as it remains with its natal pack. Perhaps older dispersers perceive more local opportunities, whereas younger dispersing animals feel less secure once they leave the fa-

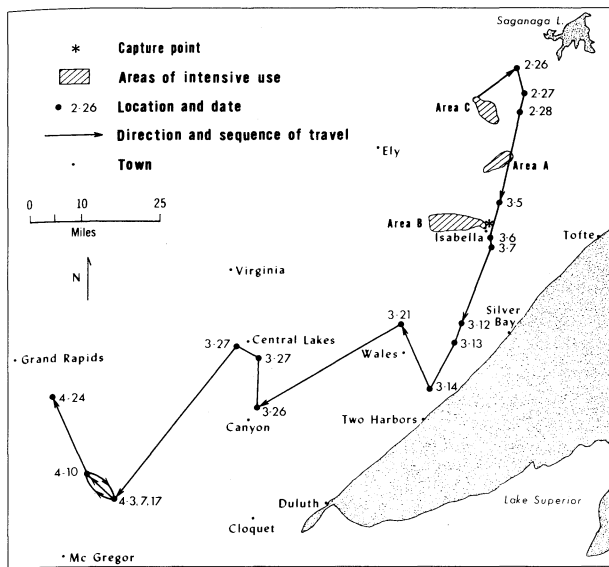


FIGURE 1.5. Dispersal of male wolf 1051 in the Superior National Forest of Minnesota. Lines merely indicate the sequence of locations. Only selected lakes are shown. (From Mech and Frenzel 1971.)

miliarity of their immediate social and physical surroundings. A 10-month-old wolf, for example, would only have had about 5 months of familiarity with its pack's territory and its immediate neighbors. Its naivete as it wanders through unfamiliar regions might drive it increasingly farther as it continues to seek security in wolf-free areas.

Wolves that disperse long distances appear to travel intently (Mech and Frenzel 1971a) in a manner that seems goal-directed (fig. 1.5). Whether the goal is to reach a particular kind of area, find a certain set of conditions, or travel a certain distance before settling is unknown. This type of travel is similar to that of translocated wolves when homing, a behavior that adults are good at if translocated less than about 130 km (80 mi) (Weise et al. 1979; Fritts et al. 1984; L. D. Mech, unpublished data). One possible deduction from this mode of travel is that wolves unable to find a breeding position locally are predisposed to proceed in a certain direction, possibly for a certain time or distance, before looking for a place to settle.

That the predisposition (Howard 1960) to distant dispersal might be genetic is an intriguing possibility. Gese and Mech (1991) found little evidence for genetic similarities in dispersal tendencies among the seventy-five dispersers they studied. However, consider two anec-

dototal cases. In Montana, two wolves 1 year apart in age dispersed 9 months apart and ended up 150 km (90 mi) away in the same pack 3 years later (Boyd et al. 1995). In Minnesota, two wolves caught 5 km (3 mi), but 12 years, apart were killed some 272 km (163 mi) away, 10 years, but only 11 km (7 mi), apart (Mech 1995e).

Some wolves disperse long distances as soon as they leave their pack, while others float around the natal population first (Mech and Frenzel 1971a; Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Messier 1985b; Mech 1987a). Both floaters and distant dispersers can be found in the same litter (Mech 1987a), but why some wolves disperse long distances without first floating is unknown.

In addition, some wolves just float without ever dispersing long distances. A good example is male wolf 75 from the SNF study, who spent his life in an area of about 1,288 km² (L. D. Mech, unpublished data). Born in 1987, this wolf paired serially with females in two neighboring packs from 1989 through 1995. Even though each female survived, male 75 left each one, then serially paired again with two females that eventually were killed; wolf 75 was then killed himself when with his sixth female in late 1996 (all the deaths were human-caused). Other wolves in this area have floated around a region of 2,550 km² (996 mi²) (Mech and Frenzel 1971a).

Dispersal Direction

Care must be taken in analyzing wolf dispersal directions because dispersal data, especially final locations of dispersers, are often obtained from harvesting programs or other wolf studies. Such information is greatly biased toward areas where wolf retrieval is most likely. The dispersal directions reported for Denali wolves may suffer from such a bias (Mech et al. 1998).

In homogeneous habitat types, wolves would probably disperse equally in all directions. However, no habitat type is homogeneous, and topography, wolf density, and areas of human development no doubt play varying roles in steering dispersal direction. For example, most northwestern Montana dispersers settled north-northwestward in a narrow swath along the Rocky Mountain chain where there were other wolves (Boyd et al. 1995). It seems significant that few wolves inhabited the areas south, east, and west of this dispersal corridor.

We might conclude from the Montana data that wolf dispersal tends to be adapted toward maximizing the

dispersers' chances of breeding rather than toward locating maximal resources. Thus, instead of dispersing toward areas of few wolves but much prey (e.g., south), the Montana wolves dispersed toward established wolf populations to the north (Boyd et al. 1995). Similar information from Wisconsin seems to show the same pattern (Wydeven et al. 1995). In other regions, however, both male and female wolves have dispersed long distances into wolf-free areas. For example, the Norway-Sweden wolf population apparently was begun by dispersers from a breeding population in Finland or Russia, more than 1,000 km (600 mi) away (Promberger, Dahlstrom et al. 1993, but cf. Sundqvist et al. 2001). In North and South Dakota, dispersed wolves have been found as far as 561 km (337 mi) from known breeding packs (Licht and Fritts 1994). A radio-collared male wolf from Michigan dispersed to Missouri, a 720 km (450 mi) move that took him hundreds of kilometers from any wolf population (J. Hammill, cited in Hutt 2002).

In the SNF, where the wolves studied were part of a larger surrounding population, yearling and adult dispersers initially headed in all directions. Pups and females settled significantly more to the southwest, and males to the north, for reasons unknown (Gese and Mech 1991). Lake Superior, lying some 35 km to the southeast, probably biased dispersal direction.

The wolves that recolonized France about 1994 no doubt dispersed from central Italy through the Apennine Mountains (Lequette et al. 1995). The relative isolation of the habitat type along the mountains, compared to the areas of high human disturbance surrounding it in the plains, probably helped funnel dispersing wolves toward France and sped up the recolonization.

Finding a Mate and Territory

As indicated above, dispersing wolves must ultimately find and acquire three things to succeed in life: a mate, food resources, and an exclusive area. A disperser can meet these needs by killing or usurping an established breeder, but it risks getting killed itself. It can also join a pack and lure out a mate, but it must then either disperse again to an unoccupied area or "carve out" a territory from the existing territorial mosaic, another risky strategy. Or it can disperse to the edge of the population range, locate a mate doing the same thing, set up a territory, and expand the species' range (Fritts and Mech 1981; Wabakken et al. 2001).

Where wolves are harvested, territories are left vacant and pack social structure is fragmented. This greatly enhances opportunities for budding wolves, floaters, and near and distant dispersers to succeed in meeting their life requirements. Thus it is common for harvested or controlled wolf populations to recover within a few years after harvesting stops (Ballard et al. 1987; Hayes and Harestad 2000a).

When most of the recent wolf studies using radio-tracking were being conducted, from the late 1960s through the mid-1990s, wolves in many areas were living in remnant populations, were legally protected, and were expanding their range. Thus considerable information is available about wolves dispersing to the edges of their range. However, under natural conditions, when wolves inhabited all of their range, such dispersal would have been rare. Floating, usurping, and other local breeding strategies would have predominated, as in many of the longer-established wolf populations in Alaska, Canada, and Minnesota. With such strategies, the actual detection of any potential mates, unused resources, and unoccupied territories would be prompt and direct.

Along the edges of the species' range, wolves might resort to more indirect means to evaluate their chances in an area. Through their daily hunting, they would learn whether the area provided enough catchable prey to support them and their offspring. In addition, they could determine through checking for scent marks and howling whether wolves occupied the area and whether there were potential mates there (see Harrington and Asa, chap. 3 in this volume).

Lone wolves in wolf-free areas tend to scent-mark and howl (Ream et al. 1985; R. P. Thiel, unpublished data), whereas those traversing wolf-inhabited areas tend not to (Rothman and Mech 1979; Harrington and Mech 1979). Presumably loners on the edges of wolf range need to advertise their presence, whereas those in wolf-inhabited areas must conceal their presence for fear of being harassed or killed.

Little is known about how wolves find mates, but the process probably takes only days once two predisposed individuals frequent the same region. The first wolf Mech ever radio-tracked, a dispersing male, in 1 week traveled more than 74 km (44 mi) and located a probable female along the edge of the species' range (Mech and Frenzel 1971a).

Information from northwestern Minnesota's expanding wolf population, where most wolves were settling lo-

cally, is instructive here (Fritts and Mech 1981). Six of seven dispersers paired within 8–30 days of leaving their packs, whereas three wolves radio-collared as loners that had already dispersed, possibly from outside the area, took longer (95–148 days). This difference could mean that pre-dispersers might be influenced to leave their pack by the presence of potential mates hanging around their area.

Pairing Success

Generally, dispersing wolves of both sexes have a high rate of success in settling and pairing in new areas (see above). Most studies indicating this involved populations that were expanding or were harvested (Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987). Nevertheless, the same was true even in the relatively protected central SNF population of Minnesota. Although dispersal rate there varied with phase of population trend, the pairing success of dispersers remained the same whether the population was expanding, declining, or stable (Gese and Mech 1991). In north-central Minnesota, where the population was subject to moderate human harvesting, all seventeen dispersers in one study settled within 267 days of leaving their pack and found potential mates (Fuller 1989b).

Dispersal beyond the Frontier

Some wolves become true pioneers by dispersing far beyond the frontier of their population. Examples include thirteen wolves killed in the northwestern United States from 1941 to 1978 (Nowak 1983), ten killed in North and South Dakota from 1981 to 1992 up to 561 km (337 mi) away from any breeding wolves (Licht and Fritts 1994), and a Minnesota disperser killed by a car in Wisconsin at least 80 km (48 mi), and probably 200 km (120 mi), from the nearest other wolves (Mech, Fritts, and Wagner 1995; see also Wabakken et al. 2001).

These pioneering wolves do not necessarily travel nomadically over a large area seeking mates. They may just disperse a long distance and then settle. In the Glacier National Park area of northwestern Montana, some 160–400 km (96–240 mi) from the nearest known wolf population, a lone female was radio-tracked over a region of about 1,100 km² (430 mi²), but concentrated her movements in two smaller areas, rather than moving nomadically over this extensive region (Ream et al. 1985).

Although the chances of distant dispersers finding a mate are small, if they do finally pair, they can begin a new population far from any source (Wabakken et al. 2001). About 20 months after the Montana female's radio collar expired, tracks of a pair were found in the area (Ream et al. 1985).

Multiple Dispersal

Although wolf dispersal typically occurs when animals are maturing, and involves a single move to a new area, some individuals may disperse and settle twice or more (Boyd et al. 1995). It is even conceivable that multiple dispersal is far more common than realized, but merely undetectable with radio collars that typically last no longer than 4 years.

In the SNF, for example, male wolf 75 dispersed from his natal pack as a yearling, lived in three other packs during the next 6 years, then successively paired with (traveled consistently with) two lone females in the next year, drifted as a loner again, then paired with another female before finally being killed by a vehicle at the age of 9.5 years (L. D. Mech, unpublished data). Two examples of male wolves dispersing and moving to successive packs were seen in Denali National Park (Mech et al. 1998).

Multiple Pack Affiliation

A few wolves associate with more than one pack more or less at the same time, but little is known about this behavior (Van Ballenberghe 1983a). It is best documented in a recolonizing population in northwestern Montana. There, "two individuals [both sexes] traveled freely between two packs and were observed caring for pups in two packs during one denning season" (Boyd et al. 1995, 139). As discussed below, such cases may involve related packs.

Colonization

The history of the northwestern Montana wolf population lends much insight into the colonization process. A few months after the tracks of a pair of wolves were found in the area, a litter of pups was born there in 1982 (Ream et al. 1991). Within the next few years, a total of about seven more founders arrived in the area, and the population had reached seventy wolves by 1996 (E. E.

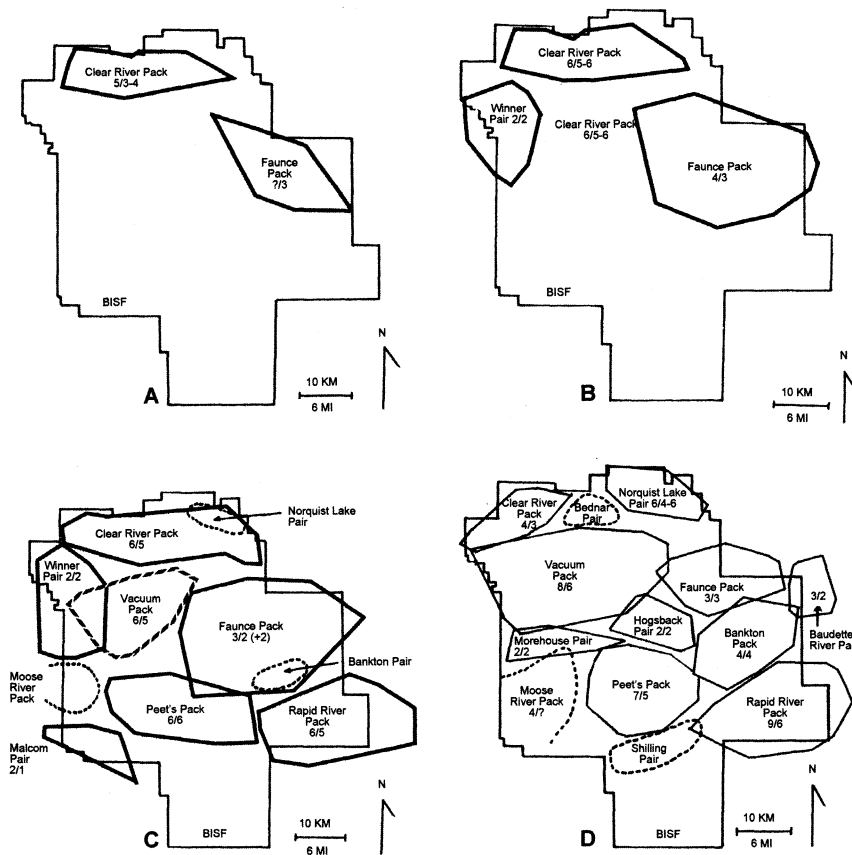


FIGURE 1.6. Proliferation of a colonizing wolf population in northwestern Minnesota. Numbers above the slashes indicate pack size in winter; numbers below the slashes indicate pack size in spring. Solid lines indicate the minimum area occupied by a pack; dashed lines indicate the approximate locations of non-radio-collared packs. (A) Size of and minimum area occupied by Clear River pack and Faunce pack in 1972–1973. (B) Size of and minimum area occupied by Clear River pack, Faunce pack, and Winner pair in 1973–1974. (C) Sizes of and areas occupied by ten social units of wolves in 1974–1975. (D) Sizes of and areas occupied by thirteen social units of wolves in 1975–1976. (From Fritts and Mech 1981.)

Bangs, personal communication). A similar process was seen in Scandinavia (Wabakken et al. 2001).

As wolves colonize or recolonize an area, the first pack soon begins to proliferate if conditions are favorable. The process of pack proliferation in Montana was similar to that in northwestern Minnesota, where, from 1972 through 1976, the number of packs increased by at least eight as a wolf population recolonized that area (fig. 1.6). Similar processes took place during population increases on Isle Royale (Peterson 1977; Peterson and Page 1988) and on Alaska's Kenai Peninsula (Peterson, Woolington, and Bailey 1984).

At least part of the pack proliferation process is fostered by dispersers from the original pack or packs (Fritts and Mech 1981). Conceivably, the first new breeders may be related animals, as they are on Isle Royale (Wayne et al. 1991). However, it is also possible, and we believe probable, that the mates of local dispersers from a colonizing pack are usually new immigrants (Forbes and Boyd 1996) that have gravitated to the territories of the original founders and helped them proliferate into

adjoining territories, as Hayes and Harestad (2000a) also suggested.

In Sweden (Björvall 1983; Wabakken et al. 2001) and in Wisconsin (Wydeven et al. 1995), the recent wolf recolonizations proceeded in several disjunct areas as well as proliferating from one core. This may have been because both these ranges contain “islands” of wilderness interspersed with agricultural and settled areas, unlike northwestern Minnesota and northwestern Montana. The recolonization of the French Alps, while still under way, shows a similar pattern (L. Boitani, unpublished data).

A year after a female wolf in Sweden reached a male that had been there for a few years, the two began producing pups in 1983 and disseminating long-distance dispersers, which then settled in new areas far from the core (Promberger, Dahlstrom et al. 1993). Despite considerable human-caused mortality, wolf numbers in Sweden and neighboring Norway had reached about thirty animals by 1994 (Wabakken et al. 2001).

In northwestern Wisconsin, which wolves began re-

colonizing in the mid-1970s (Thiel 1978; Mech and Nowak 1981), a cluster of four contiguous territories had been formed by 1979 (Wydeven et al. 1995). From 1979 to 1991, the wolves settled widely separated suitable areas (areas of low human accessibility), then gradually began filling in areas among them (Wydeven et al. 1995).

Because the wolves colonizing Sweden and Wisconsin had to have originated in wilderness, they probably selected disjunct wilderness areas in which to settle. Or, conceivably, any that tried to settle in unsuitable areas near existing packs were killed by humans. In both Sweden (Wabakken et al. 2001) and Wisconsin (Wydeven et al. 1995), humans caused much of the wolf mortality that occurred during colonization.

Of considerable interest is the observation that, during colonization, some wolves disperse out of the colonizing population foci and travel long distances through both wolf-free and wolf-inhabited regions (Fritts and Mech 1981; Wydeven et al. 1995; Boyd et al. 1995). It would seem more logical for them to settle locally, given the abundance of seemingly suitable areas available, where in fact other wolves do settle. Their failure to do so may evince a genetic predisposition for distant dispersal. The possibility that these wolves disperse far to seek unrelated mates tends to be negated by their passing through wolf-inhabited areas, where presumably unrelated candidates would be available. (See Mech 1987a for further discussion of distant dispersal.)

The Yellowstone National Park wolf reintroduction of 1995 provided interesting observations of wolf dispersal into an area with no breeding wolves. Male wolf R12 from the Soda Butte pack dispersed in January 1996, after the pack had been settled in a territory for 9 months. He then traveled in a semicircle that reached areas about 100 km (60 mi) southeast, 175 km (105 mi) south-southeast, and 240 km (144 mi) south of his pack territory before he was illegally killed (M. K. Phillips and D. W. Smith, personal communication). Conceivably, the animal was seeking out other wolves, and after not finding any after a certain distance, was continuing in a broad circle around his dispersal point.

Territoriality

Wolves generally are highly territorial (Mech 1973, 1994a; Van Ballenberghe et al. 1975; Fritts and Mech 1981; Jordan et al. 1967; Peterson 1977; Peterson, Woolington, and Bailey 1984; Messier 1985a; Ballard et al. 1987; Fuller 1989b; Ream et al. 1991; Meier et al. 1995; Mech et al.

1998). The development of territoriality is thought to depend on the influence of competition, the economic defensibility of resources, and the adaptive value of aggressiveness (see below) in relation to variation in these factors (Brown 1964).

The adaptiveness of territoriality has been explained as follows: "Territoriality is a very special form of contest competition, in which the animal need win only once or a relatively few times. Consequently, the resident expends far less energy than would be the case if it were forced into a confrontation each time it attempted to eat in the presence of a conspecific animal" (Wilson 1975, 268).

This explanation seems appropriate for wolves, for their territories encompass large areas replete with high numbers of prey. As wolves circulate about their territories seeking prey they can catch and kill, they rarely encounter neighbors, even along the edges of their territories. One of the main reasons they do not is that their territories are often so large (tens to thousands of square kilometers) that chance alone minimizes the possibility (see below).

A case has been made that wolf territorial patterns "arise naturally as steady state solutions" to the mediation of wolf movements and behavior by the presence or absence of foreign scent marks (Lewis and Murray 1993, 738). According to this theory, wolf movement is primarily dispersive, and marking frequency is low, in the absence of foreign marking, but with foreign marking, movement is toward an organizing center, and scent marking increases. The theory assumes that marks lose strength with age (Peters and Mech 1975b). A new model yields distinct home ranges through interaction between scent marking and movements in response to familiar marks (Briscoe et al. 2002).

Implied in the concept of territoriality is the need for defense, for a territory, by definition, is a defended area (Burt 1943). In theorizing about the implications of territoriality from an evolutionary perspective, various workers have uncovered several problems that a territorial species must solve. For example, defending a territory must be energetically efficient (Brown 1964), and defense must not take so much time or energy as to hamper courtship, copulation, and care of young (Wilson 1975).

The need to solve these problems is especially acute for a species with such large territories as the wolf's. However, the wolf has evolved very successful physical and behavioral solutions. The key to the wolf's solutions

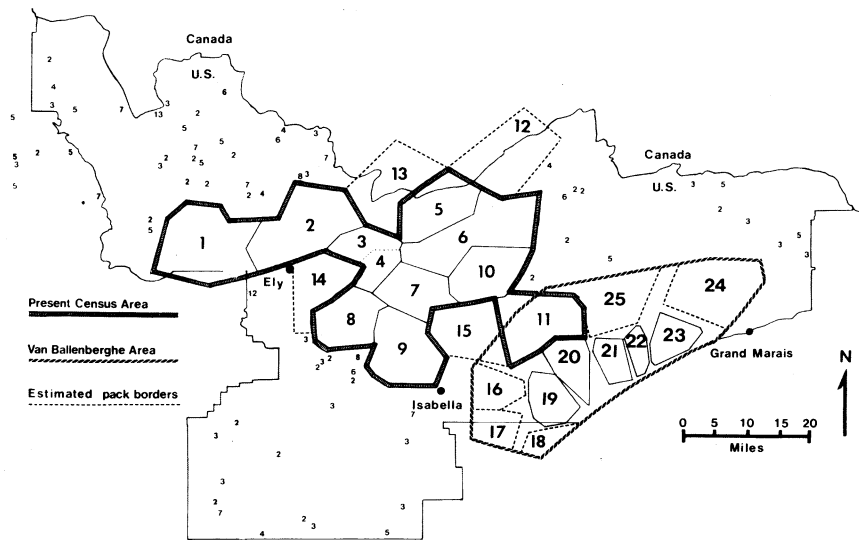


FIGURE 1.7. Wolf pack territories as first delineated in the Superior National Forest of Minnesota. Large numerals identify wolf packs, and lines around them indicate approximate pack territory borders. Small numerals represent the sizes of packs, or numbers of tracks, observed outside of the intensive study areas (lone wolves were not plotted). (From Mech 1973.)

is the ability and inclination to travel far and wide. The animal's physical stature, long legs, blocky feet, and powerful muscles allow it to travel tirelessly at about 8 km (5 mi)/hr for many kilometers per day in all sorts of climatic conditions (Mech 1966b, 1970, 1994a).

Widespread and regular travel functions both to help the wolf secure prey (see Mech and Peterson, chap. 5 in this volume) and to mark its territory (see below). Even a territory as large as 1,600 km² (625 mi²) (Mech 1988a; Meier et al. 1995) has a diameter of only about 40 km (24 mi). Wolves can cover this distance in less than a day (Mech 1966b, 1970). Since wolves both hunt and mark as they travel, and since marks are effective for long periods (Peters and Mech 1975b), this behavior allows efficient territorial defense. Howling at various locations along their routes, including homesites, complements this defense (see below).

In a well-established wolf population, a territorial mosaic develops (fig. 1.7). Each pack competes with neighbors for space and resources, and considerable territorial tension characterizes the population. The natural expansion tendency of each individual wolf has long been recognized (Schenkel 1947), and this trait expresses itself among packs as well. This expansion tendency allows the wolf population to adjust constantly, as a "flexible strategist" (von Schantz 1984), to variations in prey availability.

Each pack territory can in some respects be considered a mini-ecosystem, although not to the extreme degree Haber (1977) postulated. The size of a territory,

the abundance of prey there, and the size of the pack occupying the territory are interdependent, consistent with the resource dispersion hypothesis (D. W. Macdonald 1983) discussed above, and these characteristics are unique for each territory.

Territory Size

A wolf pack's territory and home range are the same, since the territory is the defended home range. Home range size generally is related to an animal's size (McNab 1963), and body size explains about 75–90% of the variation in carnivore home range size (Harestad and Bunnell 1979). For wolves, however, this postulated relationship predicts a territory four times the size of the average home range used ($n = 30$) in helping derive the relationship. Thus the postulated relationship applies in only a very general way to wolves and provides little information about why wolves use the size territories they do.

Most mammals have little trouble finding and processing food, so it is not surprising that there is a general relationship between body size and home range size. In general, the larger the animal, the more food it requires, and the larger the area it needs to acquire that food. However, because wolves must hunt far and wide for prey they can catch and kill, it takes a disproportionately large area to support enough vulnerable prey (see Mech and Peterson, chap. 5 in this volume). Furthermore, both prey populations and prey vulnerability can fluctuate by

orders of magnitude, and some prey are migratory or nomadic, greatly influencing the area a pack may need to cover.

Wolf pack territories vary in size by orders of magnitude. Estimated territory size depends considerably on the number of points used to define the territory, the period over which the points were derived (Fritts and Mech 1981; Scott and Shackleton 1982; Bekoff and Mech 1984; Mech et al. 1998), and the method used to analyze the points. Thus data from various studies are only roughly comparable. Nevertheless, the comparisons that can be made are instructive (Okarma et al. 1998).

The smallest well-documented territory reported seems to be that of the Farm Lake pack of six in north-eastern Minnesota, which occupied an estimated 33 km² (13 mi²) (88 locations) (L. D. Mech and S. Tracy, unpublished data). At the other extreme, Denali National Park's McKinley River pack of ten inhabited a 4,335 km² (1,693 mi²) territory (51 locations year-round) in 1988 (Mech et al. 1998), and another Alaskan pack of ten covered some 6,272 km² (2,450 mi²) in a 6-week period (calculated from Burkholder 1959).

Some wolves make grand excursions over areas of over 100,000 km² (38,000 mi²) (P. C. Paquet, personal communication), but they are not considered here because the areas they cover do not seem to be defended. In addition, migratory wolves that follow migratory caribou herds (see below) occupy areas averaging 63,058 km² or 24,600 mi² annually (Walton et al. 2001).

Territory Size and Pack Size

In establishing a territory, a pair of wolves must select an area far larger than they themselves would need to gain a living (Peterson, Woolington, and Bailey 1984), because they can expect to produce an average of five or six pups per litter (Mech 1970), which they must feed. When pups are only 6 months old, they consume as much as adults (Mech 1970), which means that pack size and resource needs suddenly quadruple. Furthermore, some packs include not only a pair of parents and a litter of pups, but also offspring of earlier years, increasing pack size by a factor of up to fifteen. Thus a pair must either establish a territory up to fifteen times as large as they require to sustain themselves, or they must later expand their territory by this much.

Wolf pairs colonizing unoccupied habitat could resort to either approach, whereas those trying to carve out territories in an existing mosaic would have to start

smaller and try to expand. In the many wolf populations that are exploited by humans, the exploitation sometimes leaves large gaps in the mosaic. There, pairs could assume full-sized territories whose occupants were recently destroyed.

Wolf pairs seem to resort to all the above approaches. On Alaska's Kenai Peninsula, where wolves are moderately exploited, two newly formed pairs established territories with areas per wolf three to four times larger than those of larger packs (Peterson, Woolington, and Bailey 1984), then maintained them as their packs grew. Hayes et al. (1991) found the same pattern in the Yukon. In Denali, the Headquarters pack maintained a territory of about 600 km² (234 mi²) as a pair in 1987 and also when there were fourteen members in 1989 (Mech et al. 1998). When pack size declines, the remaining adult pair continues to maintain a large territory (Mech 1977a).

In a newly colonizing population in northwestern Minnesota, wolf pack territories began large and were compressed considerably as more and more packs formed and began filling the available space. Not only did individual pack territories shrink by 17–68%, but one territory that began as 555 km² (217 mi²) eventually was occupied by four packs (Fritts and Mech 1981). In the Yukon, wolves recolonized an area in a similar pattern, with pack territories even overlapping after saturation (Hayes and Harestad 2000a).

It appears that the general competitiveness or aggressiveness of a pack increases with its size (Zimen 1976). By expanding a territory only slightly around the periphery, a pack could gain a considerable amount of space. For example, a territory of 250 km² (100 mi²) would have a radius of 8.9 km (5.3 mi). The addition of only 1 km more to its radius would add 58 km², or 23% more space.

However, because pairs usually establish territories large enough for a full-sized pack from the beginning, the degree of expansion necessary is not great. Thus, in most relatively intact (saturated) wolf populations, there is only a minor relationship between pack size and territory size (Potvin 1988; Fuller 1989b; Mech et al. 1998). On the other hand, where human harvesting is high and the region is not saturated, pack size and territory size may be related (Peterson, Woolington, and Bailey 1984; Ballard et al. 1987, 1997).

Territory Size and Prey Biomass

One would expect that, on average, the greater the amount of prey (prey biomass) in an area, the smaller a

TABLE 1.3. Relationship between latitude and wolf pack territory size for wolves in North America

Latitude (°N)	Mean territory size (km ²)	ml ²	Source
46	137	54	Wydeven et al. 1995
46	199	78	Potvin 1988
47	625	244	Messier 1985 ^b
48	198 ^a	77	Mech 1973
48	285	111	Fuller 1989b
48	344	134	Fritts and Mech 1981
49	69	27	Scott and Shackleton 1982
51	260	102	Carbyn 1980
56	1,028	402	Fuller and Keith 1980a
60	638	249	Peterson, Woolington, and Bailey 1984
60	795	311	Carbyn et al. 1993
61	1,645	643	Ballard et al. 1987
62	1,478	577	Hayes 1995
64	1,330 ^a	520	Mech et al. 1998
65	1,868	730	Ballard et al. 1997
70	1,225	479	Stephenson and James 1982
80	≥2,600	1,016	Mech 1988a

Note: See also Okarma et al. 1998.

^aCalculated from data presented.

wolf pack territory would need to be. Many variables would affect this relationship, such as pack size, prey size and distribution, population lags, and differences in prey vulnerability. However, overall, such a relationship should exist (Walters et al. 1981), and for wolves feeding on widely varying densities of moose (Messier 1985a) and white-tailed deer (Fuller 1989b; Wydeven et al. 1995), there is good evidence that it does. In general, about 33% of the variation in wolf pack territory size is explainable by prey biomass (see Fuller et al., chap. 6 in this volume). Further confirmation comes from a strong relationship between latitude and territory size (see next section), since prey biomass density declines with latitude. Nevertheless, this relationship is complicated by patterns of variation in prey biomass over time (both within and between years) and space (clumped or dispersed), as well as by social and other ecological variables.

Territory Size and Latitude

Even though, due to methodological differences among studies, only gross relationships between territory size

and latitude are detectable, one of the strongest links that does appear is that the higher the latitude, the larger the territory ($r^2 = .83$; $P < .00001$; table 1.3). This relationship probably results from the fact that productivity, and thus biomass density (standing crop), decreases with latitude (Rosenzweig 1968). In reality, then, this relationship is probably an extension of that between territory size and prey biomass (see above).

Territory Shape and Boundaries

Theoretically, if territory holders are competing maximally with neighbors, territorial mosaics should resemble the hexagonal cells of honeybee hives (Grant 1968; Wilson 1975). This spacing allows the maximum number of territories with the least space among them (Wilson 1975). The earliest published wolf territorial mosaic fits this model (see fig. 1.7), as do most later reports including sufficient numbers of territories (Fritts and Mech 1981; Messier 1985a; Ballard et al. 1987; Fuller 1989b; Mech, Meier, and Burch 1991; Mech et al. 1998; Hayes and Harestad 2000a).

Of course, landscape features also influence this basic mosaic structure. On Isle Royale, for example, which is 72 km (43 mi) long and 14 km (8 mi) wide, wolf pack territories tend to lie along the length of the island, but include its entire width (Peterson and Page 1988). This pattern may indicate that wolves grasp the idea of an easily defended boundary (the shoreline) and possibly some notion of the extensiveness of their territory. Otherwise, they might have divided the island up, for example, into parallel strips.

In mainland areas, topographic features such as long lakes also seem to be used as boundaries, as in the case of the Skilak Lake pack on the Kenai Peninsula (Peterson, Woolington, and Bailey 1984, 23). In the SNF Mech tracked a pack of seven to nine wolves for 2 km southward along the length of frozen Mahnommen Lake, which apparently formed their northwestern boundary. Thirteen times they had approached to within several meters of the opposite shore; each time, they had veered back toward the middle of the lake, presumably having detected their neighbor's scent marks along the shore (Peters and Mech 1975b). In other areas, wolf pack territory boundaries adjoin extensive marshes and conifer swamps where ungulate prey are not present (Fritts and Mech 1981).

Territory Shifts

The degree to which territorial boundaries are stable is an intriguing question that is not easily answered (but cf. Haber 1977). One of the main problems involves methodology. Most estimates of wolf territory boundaries are based on sampling of wolf movements by radio-tracking. However, because this is usually done via aircraft and is expensive, only a tiny proportion of a wolf pack's movements are ever sampled.

Assuming that wolves travel 20 km (12 mi) per day, for example, and that a location data point represents their location to within 200 meters, then one location per day represents 1% of that day's locations. Most radio-tracking studies gather one or two locations per week. Thus the wolf pack territories described by biologists are only gross approximations of reality. Territory sizes can be reasonably estimated by determining when any additional points in a given sample contribute insignificantly to the calculated area (Fritts and Mech 1981; Scott and Shackleton 1982; Bekoff and Mech 1984).

However, determining precise territorial boundaries

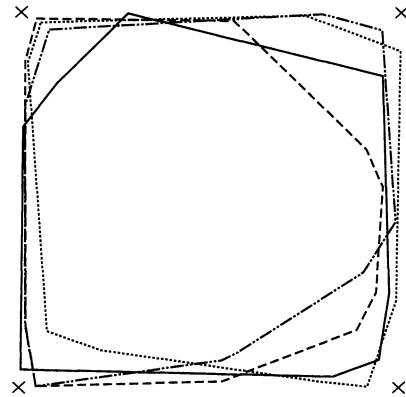


FIGURE 1.8. Varying minimum convex polygons (MCPs) resulting from four random selections of 50 points each from the same matrix of points. Note apparent differences in borders of MCPs due to sampling error. (From M. Bekoff and L. D. Mech, unpublished data.)

is impossible with standard radio-tracking. Given even a known or simulated territory, different sampling schemes produce grossly different boundaries (fig. 1.8). Thus researchers' perceptions of seasonal or yearly boundary shifts, for example, must be viewed very cautiously (Mech et al. 1998). Also, the use of old location data along with new may give an outdated or distorted picture of the current territory. (The use of Global Positioning System collars may help solve this problem: Merrill et al. 1998; Merrill 2002.) Even snow tracking cannot be relied on to yield a full understanding of a pack's territory, because rarely, if ever, does weather allow one to track wolves in the snow for months on end and thus learn the full extent of their territory.

Furthermore, there is no reason to believe that a pack territory is a constant, stable area. Rather, wolf packs in saturated populations are always competing with neighbors, defending their own areas and probably jockeying for advantages along whatever their current borders are. In exploited populations, such turbulence is no doubt accentuated.

Given all the above considerations, something can still be said about the spatial dynamics of wolf pack territories. As expected, the greatest shifts in wolf pack territories occur in colonizing or recolonizing populations. No doubt this is because of the lack of constraint by any neighboring packs. The Montana Magic pack shifted its territory 50 km (30 mi) south (Ream et al. 1991), and the Soda Butte wolves of the reintroduced Yellowstone population apparently shifted their territory back and forth

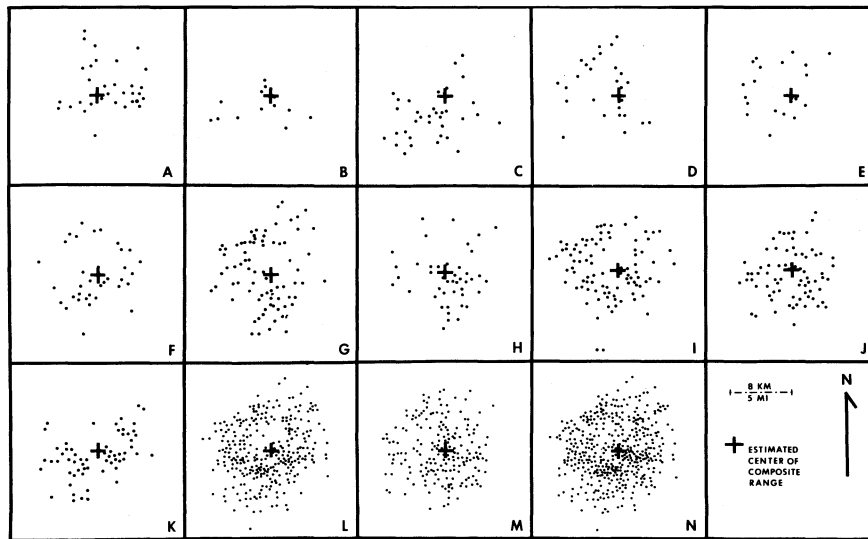


FIGURE 1.9. Distribution of locations of the Harris Lake pack in the Superior National Forest for various periods, as shown by radio-tracking: (A) winter 1968–69; (B) summer 1969; (C) winter 1970–71; (D) summer 1971; (E) winter 1971–72; (F) summer 1972; (G) winter 1972–73; (H) summer 1973; (I) winter 1973–74; (J) summer 1974; (K) winter 1974–75; (L) composite of all winters; (M) composite of all summers; (N) composite of all locations, summer and winter. (All trespasses are excluded.) (From Mech 1977a.)

over a large area (M. K. Phillips and D. W. Smith, personal communication). In both cases, these shifts could have been seasonal movements, since they occurred in autumn and could have been related to prey migrations. In the Yukon, such shifting by packs into the wolf removal area was more important in early years than later in the recolonization (Hayes and Harestad 2000a).

In the colonizing population of northwestern Minnesota, several packs shifted their territories grossly enough that the observed shifts were probably real (Fritts and Mech 1981). In some cases, the shifts were related to the formation of new packs that began filling up the available area. Hayes (1995) believed that his data showed that, during the first 2 years of his population's recovery in the Yukon, pack territories were exclusive, but that after enough territories developed, they began to overlap. Other gross shifts in wolf pack territories have been reported on the Kenai Peninsula (Peterson, Woolington, and Bailey 1984), in central Alaska (Ballard et al. 1987), in north-central Minnesota (Fuller 1989b), and in Wood Buffalo National Park (Carbyn et al. 1993).

In saturated wolf populations, of course, each pack territory is surrounded by others, so that any territorial shifts involve neighbors. Our impression is that the borders of most territories in the mosaic are constantly shifting, but that the center of each territory remains approximately the same over the years (fig. 1.9). Superimposed on this dynamism are the interactions among packs described earlier that snuff out some packs or create new territories as a wolf population fluctuates (Meier et al. 1995).

Seasonal Shifts in Territories

Because ungulates shift their movements seasonally to varying degrees, so too do the wolves that prey on them. Some territory shifts can be relatively minor, such as those within small territories where white-tailed deer are the primary prey (Van Ballenberghe et al. 1975; Mech 1977a). However, when SNF deer numbers were low during the 1970s and no deer remained in certain wolf territories during winter, those packs migrated some 50 km (30 mi) out of their usual territories. They then became nomadic around areas of up to 1,500 km² (585 mi²) before returning to their territories in spring and denning there (L. D. Mech, unpublished data). Similarly, in central Italy, wolves made small-scale shifts during summer to the sheep-grazing areas (Boitani 1986).

Migration

In some regions, wolves migrate altitudinally as prey such as elk or moose that spend the summer in high areas migrate to valleys for the winter (Cowan 1947; Carbyn 1974; Ballard et al. 1987; Ream et al. 1991). In such cases, it appears that the packs remain territorial, but just shift their territories with the movements of the prey.

Where wolf prey are highly migratory, the wolves themselves must also migrate, unless alternative prey can tide them over until the migratory prey return. The longest wolf migrations are those in which wolves follow caribou herds, at times for up to 508 km (305 mi) (Kuyt 1972; Parker 1973; Miller and Broughton 1974; Miller

1975; Stephenson and James 1982; Ballard et al. 1997; Walton et al. 2001). In Kazakhstan, wolves follow the saiga antelope herds to their wintering grounds, and in central Canada, they track the long seasonal habitat type shifts of bison (Carbyn et al. 1993).

Little is known about the extent to which wolves are territorial during migrations, or when several packs are focused around prey concentrations during winter. Although pack ranges in some such areas do overlap, wolves still kill other wolves in such areas (Carbyn et al. 1993). In Yellowstone, the newly established packs maintain different territories in summer and winter, even around the high elk concentrations that inhabit the area (M. K. Phillips and D. W. Smith, unpublished data).

Territory Buffer Zones

Most studies of wolf pack territories indicate a certain amount of overlap among territories (see also Mech and Peterson, chap. 5 in this volume). The degree to which this overlap is spatial or spatio-temporal (Mech 1970; Ballard et al. 1987) has not been analyzed, and given the problems described above with radiotelemetry sampling, such an analysis may not be forthcoming any time soon. However, biologists have tracked wolf packs in snow enough to demonstrate that, at least along the immediate territory edge, movements of neighboring packs may overlap during short periods (Peters and Mech 1975b; Peterson and Page 1988).

Given this overlap, Mech (1977d) proposed that the overlap area is a kind of buffer zone between packs. Based on the fact that during a drastic deer decline, the wolves in the SNF eliminated deer first from the cores of their territories and only last from the edges, Mech (1977a,d) deduced the existence of the buffer zone, thought to be about 2 to possibly 6 km (1.2–3.6 mi) wide (Peters and Mech 1975b; Mech 1994a). He believed that the reason deer survived longer along the territory edges might be that neighboring packs felt more threatened there, so spent less time there, and thus deer bore less hunting pressure in these areas (Mech 1977a,c) (see Mech and Peterson, chap. 5 in this volume).

Evidence that buffer zones are areas of contest comes from an analysis of locations where wolves were killed by other wolves. In the SNF, in 1968–1992, 23% of twenty-two wolf-killed wolves perished along the estimated edge of their territory; 41% were killed along the edge or within 1 km of the edge, and 91% within 3.2 km of the edge (Mech 1994a). In the Yukon, 35% of wolf-killed

wolves were killed within 2.5 km of their territory edge (Hayes 1995). In Denali, eight of twelve wolves killed by other wolves within their own territories (75%, a significant disproportion) died within 3.2 km of their estimated territory border, an area constituting only 29% of the average territory there (Mech et al. 1998). There is also theoretical evidence that buffer zones may be prey refuges (Lewis and Murray 1993) and that territorial stability in such zones would require inter-pack aggression by wolves (Taylor and Pekins 1991), which has been demonstrated (see above).

Territorial Defense

The concept of territoriality implies defense of an area (Burt 1943), and that defense theoretically should require less energy than that gained as a result of the defense (Brown 1964; Wilson 1975). The degree to which territorial defense is seasonal is unknown; however, territorial advertisement and defense tend to peak during the breeding season (Peters and Mech 1975b; Harrington and Mech 1979), as does aggression (Zimen 1976).

For a wide-ranging animal like the wolf, the problem of defending its entire home range is great. Wolves have solved this problem through a combination of at least three types of defensive behavior: scent marking, howling, and direct attacks. The first two behaviors are detailed by Harrington and Asa in chapter 3 in this volume, and will be discussed only briefly here. Both behaviors are indirect, and they complement each other in their application.

Scent Marking

Wolf scent-marking behavior used for territorial advertisement includes raised-leg urination (RLU) and perhaps standing urination (STU) by males, flexed-leg urination (FLU) and possibly squat urination (SQU) by females, and perhaps defecation (SCT) and ground scratching (SCR). Products of these behaviors are left, on average, every 240 meters throughout wolf territories, but especially along regular travelways and at junctions (Peters and Mech 1975b). Scats may carry anal gland secretions, and scratching may distribute secretions from interdigital glands (Peters and Mech 1975b; Asa et al. 1985).

Both wolf and coyote packs leave twice as many marks along the edges of their territories as in the core, resulting in an “olfactory bowl” (fig. 1.10, Peters and Mech 1975b; Bowen and Cowan 1980; Paquet 1991a; but

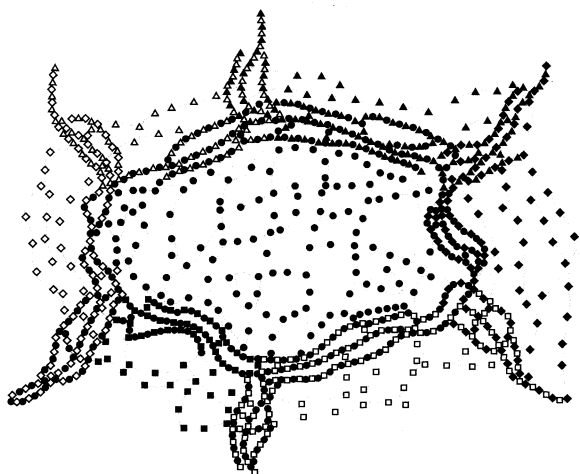


FIGURE 1.10. In this model of the distribution of raised-leg urination (RLU) scent marks, RLUs are indicated throughout the territory of one wolf pack (black dots) and for the areas where six neighboring packs border this territory. Each different symbol represents the marks of a different neighboring pack. Travel routes are simulated, but mean RLU density and territory size are to scale for a territory approximately 20 km (12 mi) wide. Note the bowl-shaped effect caused by heavier scent-marking by both the resident pack and its neighbors at the edges of the territory (Peters and Mech 1975).

cf. Barrette and Messier 1980). Scent marking appears to serve as a long-lasting (2–3 weeks) means of advertising a pack's presence.

Three aspects of scent marking imply that one of its most important functions is to deter neighbors from intruding (Peters and Mech 1975b): First, territorial packs mark, but nonterritorial animals do not. Second, packs that trespass into neighboring territories suspend marking until they return to their own territories, at least in the SNF (L. D. Mech, unpublished data). Finally, wolves are intimidated and deterred by neighbors' marks (Peters and Mech 1975b; Peterson 1977; Mech 1993a; L. D. Mech, unpublished data). There may be several other effects and functions of scent marking in relation to territorial defense, but these have yet to be explored.

Howling

The main disadvantage of scent marking as a means of advertising a territory is that it has little effect over long distances. Thus howling nicely complements scent marking. Although howling has several functions, at least one of them seems to be to inform neighboring packs that a territory is occupied (Joslin 1967; Harrington and Mech 1979).

Indications are that in forested areas, wolves can hear

howling at distances of up to 11 km (6.6 mi) (Harrington and Mech 1979) and on open tundra at up to 16 km (9.6 mi) (R. O. Stephenson, unpublished data, cited in Henshaw and Stephenson 1974; L. D. Mech, unpublished data). Observations of wolf packs howling to each other over expansive territories are necessarily rare, but territorial packs reply to human howling (Pimlott 1960; Joslin 1967; Harrington and Mech 1979).

Furthermore, wolves seem to be able to pinpoint the precise location of human howlers from distances of 2.7 km (1.6 mi), at least on tundra (L. D. Mech, unpublished data). Breeding animals tend to approach the howler (Joslin 1967; Peterson 1977; Harrington and Mech 1979), sometimes minutes after howling has stopped (L. D. Mech, unpublished data). Although no one has witnessed two packs interacting as a result of howling, the usual reaction of wolves encountering non-pack members is fighting and chasing (see below).

Direct Territorial Defense

Howling and scent marking must minimize the chances of neighboring wolves encountering one another. On the other hand, packs do sometimes meet up with each other, and these encounters often result in wolves being killed (Mech 1994a). Because the consequences of territorial encounters are so severe, and because systems are in place to avoid them, there is reason to believe that wolf territorial encounters are a result of either desperation (i.e., a wolf or wolves taking a chance for some kind of temporary gain), or deliberate aggressiveness (i.e., wolves seeking out others to kill or displace).

The main reason wolves might be desperate is probably hunger. Certainly in the SNF, the most trespassing by territorial packs deep into the territories of neighbors to kill prey was seen during a severe prey decline (Mech 1977a,b; L. D. Mech, unpublished data), and in Quebec, packs that made extraterritorial excursions were those in areas of low prey density (Messier 1985b). On Ellesmere Island, three of the five encounters that Mech and associates observed between a resident pack and outsiders involved food competition (fig. 1.11); one encounter ended in the death of the stranger (Mech 1993a; L. D. Mech, unpublished data). In Wood Buffalo National Park, a wolf pack that killed a bison in another pack's territory soon saw at least two of its members killed by the resident pack (Carbyn et al. 1993).

Deliberate attacks on neighbors represent more than territorial defense, but the tendency toward such behavior certainly must help enforce territoriality, as with



FIGURE 1.11. A breeding male wolf (right) attacks a strange wolf (left) near the edge of the breeder's territory. (From Mech 1993a.)

coyotes (Gese 2001). Forays into neighboring territories (fig. 1.12) and attacks on neighbors must be a result of a certain aggressiveness, to be discussed below. Many such deliberate attacks have been recorded (Haber 1977; Mech 1977a; L. D. Mech, unpublished data; Peterson 1977; Meier et al. 1995). In both northwestern Minnesota and Riding Mountain National Park (Manitoba), at times when there appeared to be abundant prey, wolf packs displaced neighboring packs (Fritts and Mech 1981; Carbyn 1981).

Whether encounters between packs are due to deliberate attacks or food competition, the end result is often death. As indicated above, most wolf deaths resulting from wolf attacks take place near territory boundaries or within buffer zones (see below), and killing by other wolves is one of the commonest causes of natural wolf mortality (Mech 1977b; Mech et al. 1998). Thus wolf pack territorial defense can be considered the most important feature of wolf spatial ecology.

Competition and Intraspecific Strife

“The predominant single factor tending to increase aggressiveness through natural selection should be competition” (Brown 1964, 161). Viewed on a population scale, wolf competitiveness is a pervasive phenomenon. Social competition in wolves is always intense. This contention may imply that the “ecological requisites” of wolves always exist at less than optimal levels (Brown 1964).

However, even where food is abundant and the wolf population is low—conditions that Brown (1964) claimed should minimize territorial defense—wolves are keenly competitive. Such conditions characterize colonizing populations, but even in those populations, fatal attacks are known to occur (Fritts and Mech 1981; Wydeven et al. 1995; R. R. Ream et al., personal communication). Furthermore, the three packs of reintroduced Yellowstone wolves released concurrently restricted their ranges within a few weeks and intermingled their areas

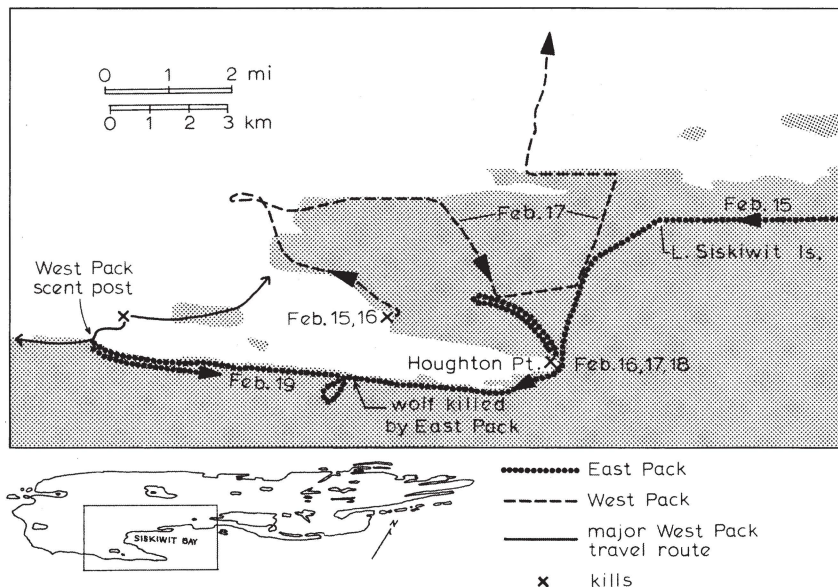


FIGURE 1.12. Movements of Isle Royale's East pack into traditional West pack territory in 1974 (Peterson 1977).

only minimally (M. K. Phillips and D. W. Smith, personal communication). Fatal aggression between members of two adjacent packs released in 1996 was observed within 6 months of release. The prey supply in the area numbered in the thousands.

It is easy to see why, in a declining wolf population with decreasing resources, the remaining members would be highly competitive. In an increasing population, too, competition should be keen because of the greater wolf numbers. The main difference between these two situations is that in an increasing population, the competitors are more likely to be kin than in a decreasing population (see above). Thus perhaps competition with close neighbors should be less intense in an increasing population.

The only observed relationship between the annual rate of wolves killed by wolves in the SNF from 1970 to 1989 (L. D. Mech, unpublished data) and population phase (Gese and Mech 1991) was that from 1978 through 1985, when the wolf population was lowest on average, intraspecific mortality was also lowest (L. D. Mech, unpublished data). This information, as well as observations of wolf packs tolerating each other when meeting (Pimlott et al. 1969), suggests that there may be periods when competition is relatively low. Most likely such times would be either when prey is surplus to the wolves' immediate needs or when relatedness among adjacent wolf packs is high. On the other hand, even when food appeared to be in surplus on Isle Royale, West pack II sought out and attacked other wolves (Peterson and Page 1988).

There is no absolute limit on competition among wolf kin, however. This is apparent within a pack when food is short; adults compete fiercely with yearlings, yearlings with pups, and pups with one another (see Packard, chap. 2 in this volume). Furthermore, on Isle Royale, where all wolves are related as closely as siblings (Wayne et al. 1991), wolves space themselves territorially and behave toward each other like any outbred population, and still kill each other (Peterson 1977; Peterson and Page 1988). This does not necessarily mean that wolves would kill close kin under other circumstances, for when all competitors are closely related, kin competition would be maximized. The only record we know of wild wolves killing close kin other than on Isle Royale involves apparent sisters in Yellowstone National Park (McIntyre and Smith 2000), although admittedly gathering such data is difficult.

Wolf aggressiveness might stem from food competi-

tion, breeding competition, or both. Nothing is known about the possibility of packs competing for breeding opportunities; however, the incidents described above in the section titled "Usurping a breeder" could be examples of such competition. In any case, analyses of deaths of wolves due to wolf attacks over a 22-year period in the SNF (Mech 1994a) and a 9-year period in Denali National Park (Mech et al. 1998) suggest that such intraspecific strife primarily represents territorial competition that reduces competing breeders and increases opportunities for packs to expand their territories, while indirectly tending to hold each pack in its territory.

This conclusion is supported by several lines of evidence. First, it is primarily maturing or mature wolves, which are the territory holders, that are killed by other wolves (L. D. Mech, unpublished data). Second, killings are concentrated in the few months before and after the breeding season (L. D. Mech, unpublished data), when chances are greatest of interfering with a neighboring pack's annual reproductive increase. Successful interference would reduce the pressure the neighboring pack would place on a pack's food supply and thus on its spatial needs. Third, some deaths involve individuals killed in their established territories by invaders. This last evidence tends to rule out strict territorial defense as the sole motive for intraspecific strife, although the territorial competition explanation obviously encompasses territorial defense.

Fates of Fractured Packs

Fractured packs are packs whose key members are lost to various sources of mortality. The fates of these packs depend a great deal on just which members are lost. Since the core of the pack is the breeding pair, the loss of any or all of their offspring means merely that the pair continues to hold the territory. Even with the loss of one member of the pair, the other member may hold the territory until a new mate arrives (see above). In Wisconsin's colonizing population, some single adult wolves that had lost a mate remained in their territories for years before finding another mate (R. N. Schultz and P. C. Wilson, unpublished data).

When the breeding pair is lost, the remaining members of the pack may disperse and join the floaters in the population (Meier et al. 1995; L. D. Mech, unpublished data), just as young members that are removed from packs and translocated behave like dispersers (Fritts et al. 1984, 1985). In one case, however, pups in their

first winter whose parents were killed by other wolves eventually starved (Meier et al. 1995). In another case, both members of the breeding pair left or were lost, and the single remaining daughter paired with a dispersed neighbor (Mech 1987a).

An instructive case involves Montana's Ninemile pack. After producing a litter of pups, both adults were killed by midsummer. Government workers artificially fed the pups. The litter remained together all summer and autumn and eventually dispersed as yearlings (Jimenez 1992).

Spatial Structure and Population Change

Because wolf population size depends so much on the amount of vulnerable prey biomass available (Packard and Mech 1980), and because that figure varies widely each year, wolf populations can also fluctuate greatly (see Fuller et al., chap. 6 in this volume). Moderate fluctuations can change pack sizes without changing the structure of the territorial mosaic (Fuller 1989b). However, large population increases are accompanied by attempts at new pack formation, as described above. Much of the dynamism in the territorial mosaic described above results from population fluctuations.

Spatial Changes during Population Increases

When a wolf population is increasing, it produces large numbers of pups (see Fuller et al., chap. 6 in this volume), which increases food competition. As those pups begin to mature, they begin competing for breeding space. This competition increases the potential for bidding, budding, splitting, dispersing, challenging, floating, and carving out new territories. Because these local territory formation strategies usually succeed during increases in wolf populations, one can conclude that established packs with adequate food can afford their territory size being reduced by competitors, so are less competitive with new packs than are food-stressed packs. This idea conforms to the elastic-disc view of territoriality (Huxley 1934) and makes sense from an evolutionary perspective.

Packs with sufficient resources should allow room for offspring so long as their own survival is not jeopardized. In fact, the above reproductive and territory proliferation strategies were observed primarily in increasing populations (Fritts and Mech 1981; Peterson and Page 1988; Meier et al. 1995), except for pack splitting, which

took place at the bottom of a population decline (Mech 1986) and at the top of an increase (Meier et al. 1995).

Based on two studies (Fritts and Mech 1981; Hayes and Harestad 2000a), the spatial changes that take place as wolf populations colonize or recolonize an area are as follows: First, pairs form large territories and breed; then pack size increases, territory size declines, and the number of territories increases. This progression of spatial and group size changes is similar to that of a fox population facing increasing food, which Lindstrom (1986) postulated was the basis for promoting group inheritance of territories. There appears to be some merit in this theory as applied to wolves in that pack budding, splitting, and multiple breeding (see above) would promote offspring remaining at home longer (philopatry). Philopatry, in turn, would further the inheritance of local resources by offspring of the original breeders.

Spatial Changes during Population Decreases

When wolf populations decrease, one might expect pack territory numbers to decrease and individual pack territories to enlarge. Although too few studies have been done on this subject to provide many details, the biology of the wolf tends instead to promote the quick proliferation of territories, but retard their decrease.

Here is why. Wolves can produce offspring at 2 years of age, so under favorable conditions, many potential breeders quickly become available seeking breeding positions. However, because breeders are productive for 8–10 years (see Fuller et al., chap. 6 in this volume), pairs established in territories must try to hold their territories for long periods, even during resource declines. Resource availability is greatly dependent on weather (see Mech and Peterson, chap. 5 in this volume), and weather can vary annually, so the chances of a pair experiencing a resource decline during their lifetime are good.

However, a wolf population can easily adjust to huge decreases in resource availability through increased dispersal of young and a reduction in productivity. For example, a pack of sixteen (two breeders, two 3-year-olds, six yearlings, and six pups) could drop almost 90% within a few months to just the two breeders merely through dispersal, and the pair could still hold its territory (see below). If necessary, the pair could then refrain from producing young until resource availability improved. Although we know of no such drastic decline, Mech (1986) has seen the Ensign Lake pack in the SNF drop from ten to two in 2½ years and Denali's East Fork

pack drop from twenty-nine to eighteen in a few months (Mech et al. 1998).

Thus, once a wolf pair establishes a territory, it strongly resists losing that area. Some individual wolves and their offspring have held their territories for 8–12 years or more in the SNF (Mech and Hertel 1983; L. D. Mech, unpublished data) and on Ellesmere Island (Mech 1995d). (This does not necessarily mean that territory boundaries remain the same for the entire period, but the territory does cover the same general area.) On the other hand, there is some evidence that only a small percentage of packs hold their territories any longer than this (see below).

The history of the Isle Royale wolf territorial mosaic perhaps illustrates more dramatically than any other case the tendency of established breeders to continue holding territories. Wolves colonized the Lake Superior island in 1949. Little information about pack territories was recorded before 1959, but in that year one large breeding pack of fifteen dominated the island (Mech 1966b). Not until 1965 did a second breeding pack bud from the first (Jordan et al. 1967). However, ever since then, there have been two to four pack territories on the island, even after the population fell from fifty wolves to twelve (Wolfe and Allen 1973; Peterson 1977; R. O. Peterson, unpublished data; Peterson and Page 1988).

The only other population under primarily natural regulation that has been studied throughout a drastic decline in wolf numbers is the central SNF study population. It fell from eighty-seven wolves in 1969–70 to forty-four in 1974–75, and during this period the number of packs dwindled only from thirteen to eleven (Mech 1986). One of the lost packs resulted from the fight between and apparent merging of the Pagami and Greenstone packs, described above.

Relatedness among Packs

As should be apparent from the preceding sections, neighboring wolf packs tend to be genetically related. The closer one pack lives to another, the greater its chance of being related to the other. This tendency results from the budding and splitting processes constantly under way in a vigorous population, as well as from attempts by dispersed offspring to fill in interstices among pack territories. Molecular genetic data (Lehman et al. 1992) confirm the field data based on known wolf demographics (Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987; Meier et al. 1995).

Conceivably, the phenomenon of wolves living with more than one pack (Peterson, Woolington, and Bailey 1984; Mech 1987a; Ream et al. 1991; Boyd et al. 1995; see above) is explained by the close genetic relationships between certain packs in a population. On the other hand, it may be the cause of that close relationship. One male wolf that was known to live intermittently in his natal pack and in a neighboring pack over a 20-month period eventually moved into the neighboring pack and paired with a female there (Mech 1987a).

Nevertheless, the constant churning of the population resulting from strong competition and intraspecific strife (see above), as well as from the immigration of dispersers from distant populations, continues to ensure a certain level of unrelatedness.

One could theorize that expanding populations tend to be more closely related, on average, than contracting ones, for the reasons discussed above. Certainly the wolves in the best position to increase their genetic contribution to the population would be those occupying territories when prey availability increases. Because of the wolf's tendency to outbreed (D. Smith et al. 1997), however, a countertendency would develop, guaranteeing a constant influx of new genes and diluting the relatedness of the population (Kennedy et al. 1991; Lehman et al. 1992). The direct killing of breeders by neighbors (see above) tends not only to increase genetic heterogeneity, but to accelerate its increase (Mech 1977b).

Movements within Territories

Wolf travel within territories serves two main functions: foraging (hunting, scavenging, and food delivery) and territory maintenance. Travel would be most efficient if it were used for both functions, and there is every indication that this is the case. Whenever we have watched wolves traveling, they were both foraging and marking.

Wolves generally follow trails, shores, gravel bars, frozen waterways, ridges, roads, and other types of terrain that are easy to traverse. Even in closely cropped pastures and on frozen lakes, any part of which might seem to be an easy route, wolves still tend to follow trails or tracks of other animals. We have often thought this tendency may facilitate travel by allowing the wolves to concentrate on their surroundings rather than constantly having to focus on where to place their feet. Wolves generally travel single file, and in deep snow, this pattern allows more efficient travel by the younger individuals, which usually follow their parents.

Wolf movements within a territory differ between the pup-rearing season, spring to early fall (see Packard, chap. 2 in this volume), and the rest of the year (Mech 1970; Mech et al. 1998; Jedrzejewski et al. 2001). When rearing pups, pack members radiate out from the den or rendezvous site where the pups are to other areas of the territory, returning periodically to feed and care for the pups (Murie 1944; Chapman 1977; Haber 1977; Mech 1988a). Once the pups are developed well enough to join the adults on their hunts, the pack moves as a unit and becomes nomadic around the territory (Burkholder 1959; Mech 1966b; Peterson 1977; Musiani et al. 1998; Jedrzejewski et al. 2001). However, wolves occasionally use rendezvous sites even when offspring are as old as 13 months (Mech 1995c), and in central Italy, where wolves coexist with extensive human activities, they tend to maintain rendezvous sites year-round, radiating out from them at night (Boitani 1986).

Locations of Homesites in Territories

One might expect that wolf dens and rendezvous sites (see Packard, chap. 2 in this volume) would be located toward the center of the pack territory (Banfield 1954; Ballard and Dau 1983). Such a location would maximize the ability of adults to forage efficiently in all directions and minimize exposure to neighboring packs.

However, this hypothesis was not fully supported in the SNF (Ciucci and Mech 1992). Instead, wolves denned more or less randomly throughout their territories except for the outer 1 km, which seems to have been avoided. For wolves denning in the central 60% of their territories, however, there was evidence that the larger the territory, the closer to the center the wolves denned. Similar analyses are needed for other areas.

Where humans persecute wolves, the animals tend to locate their dens far from human disturbance. However, where wolves have not been persecuted for many years, they may den close to areas of high disturbance (Thiel et al. 1998). Rendezvous sites are usually located in the general denning region, so den location is the strongest determinant of their location in a territory.

Movements during the Pup-Rearing Period

Once wolves have denned, the social center of the pack is usually the pups (Murie 1944; Mech 1970, 1988a; Clark 1971; Haber 1977; Jedrzejewski et al. 2001). The reason for this is simple: The breeding pair's entire annual repro-

ductive investment is in the pups, which require regular care and feeding. Thus the parents must return to the pups as frequently as possible after foraging. Other pack members are also tied to the den area not only because they contribute to the care and feeding of the pups (see Packard, chap. 2 in this volume), but also presumably to maintain their bonds with the breeding pair and one another.

There are two exceptions to this generalization. First, maturing pack members sometimes leave the pack for varying periods and return much later (see above). Second, occasionally a large contingent of the pack, sometimes including the breeding male, lives nomadically while the breeding female, or the breeding female and a maturing offspring, feed and care for the pups (Mech et al. 1998). (Females have been known to raise pups alone, although no doubt they would not always be as successful as two parents; see Packard, chap. 2 in this volume.)

Wolves may travel as far as 48 km (29 mi) from the den or pups to obtain food (Mech 1988a). When Mech (1988a, 1995c,d) accompanied a habituated pack of wolves on Ellesmere Island during their hunts away from the den, he noticed no difference in their travel rates or patterns from those of nomadic packs in winter (Mech 1966b). The wolves basically traveled from prey concentration to prey concentration until they killed something. The difference, then, was that wolves with pups returned to the den soon after gorging.

Little is known about the patterns of post-denning territory use. However, there is little reason to think that wolves would use their territory any differently once they have left the den, although there is evidence of seasonal changes in territory use (Jedrzejewski et al. 2001; Merrill 2002). The relative extensiveness of territory use during the pup-rearing season versus the rest of the year seems to vary by study, and one must be cautious in interpreting these data because of the sampling problem discussed earlier (see "Seasonal Shifts in Territories").

Homesite Shifts

As the pups grow and develop, the adults may move them from one den or rearing site to another over the summer (see Packard, chap. 2 in this volume). When the pups are young, these moves may be as short as 0.25 km, whereas as they get older, such moves may be as far as 8 km (5 mi) (Joslin 1966; L. D. Mech, unpublished data). In one case, which may be an exception because

it involved a pack with only a single 8-week-old pup, the Ellesmere Island pack shifted rearing sites some 32 km (19 mi) (L. D. Mech and L. Boitani, unpublished data).

Movements during the Nomadic Phase

Generally, wolves are nomadic during about half the year, after their pups have grown and developed enough to move with them. At least one study has suggested that the first movements of the nomadic phase are perhaps the most extensive of all (Fritts and Mech 1981). The most instructive information about movements during the nomadic phase derives from aerial snow tracking of wolves (Burkholder 1959; Mech 1966b; Jordan et al. 1967; Haber 1977; Peterson 1977). Much of this work was done on Isle Royale in Lake Superior, which has a long and narrow configuration. Although this fact should have little effect on such parameters as rate and distance of travel, it would affect the rate of doubling back, for example, and possibly other parameters.

Speed

Wolves usually travel at a lope. Since they are narrow-chested, and since their elbows are turned inward and their feet outward (Iljin 1941; Young and Goldman 1944), they put their feet one almost directly in front of the other as they walk. They can maintain this tireless gait for hours at a rate of about 8–9 km/hr (Burkholder 1959; Mech 1966b, 1994b; Shelton 1966). At times they break into an exuberant run at perhaps twice this speed, presumably in anticipation of something ahead. When returning to the den, their average speed increases to 10 km/hr (Mech 1994b). The wolf's elongated muzzle and the shape of the inner nose ensure optimal oxygenation and an efficient cooling system even in hot climates.

Distance

As already indicated, wolves are capable and inveterate travelers. Some of the claims for their travel distances may be exaggerated, such as J. Magga's that, when hunted, wolves can travel 200 km (120 mi) in a day (Pulliainen 1965); on the other hand, at only their usual rate of 8 km/hr, they could do so. What we do know is that in winter, packs can travel up to 56 km (35 mi) overnight (Stenlund 1955) and up to 72 km (45 mi) in 24 hours (Burkholder 1959; Pulliainen 1965; Mech 1966b; Pimlott et al. 1969). On average, wolves on Isle Royale traveled

14.4 km (9 mi) per day in winter (Mech 1966b). Even in territories of 172–294 km² (67–115 mi²) in Poland (Okarma et al. 1998), wolves traveled a mean of 22.8 km (13.7 mi) per day (Jedrzejewski et al. 2001). In Italy, wolves averaged 27.4 km (16.4 mi) per day (Ciucci et al. 1997).

The usual pattern of winter wolf movement includes travel for a long distance while hunting, making a kill, feeding, resting, and local movement near the kill, abandoning the kill, and repeating the cycle. When all elements of this pattern are considered, wolves cover their ranges at an average of about 2.4 km/hr (Mech 1970). This rate includes an actual travel rate while hunting of about 50 km (30 mi)/day, and an average of about 30% of the wolves' time is spent hunting (Mech 1970).

If wolves fail to produce pups, or lose them, the adults remain nomadic during summer (Mech 1995c), and their rate and distance of travel is similar to that during the rest of the year (Mech 1988a, 1994b, 1995c). One would expect that during summer wolves would need to rest less, since they would not be wading through snow. If so, they probably can cover more distance, although the only information available on this subject is from the SNF, where wolves averaged 19 km (11 mi) per day, with a range of 7–46 km (4–28 mi) per day (D. J. Groebner and L. D. Mech, unpublished data).

Differential Use of Habitat Types

Wolves gravitate to areas within their territories where prey live. Each prey species uses habitat types differently. White-tailed deer, for example, space themselves widely over a variety of habitat types in summer, but yard up in winter in protected lowlands or on south-facing slopes. Dall sheep tend to frequent the steepest mountain terrain and venture into the lowlands only to get to other mountains. Thus, during their routine hunting trips, wolves tend to travel wherever the prey reside in their territory and to avoid prey-free areas, such as extensive conifer swamps (Fritts and Mech 1981) and mountains in winter when prey inhabit valleys (Ream et al. 1991). In the Caucasus Mountains of Europe, an observer following wolf routes counted five to fifteen deer and several wild boar per hour, whereas a random route showed no more than five or six animals per hour (Kudaktin 1979, cited in Bibikov et al. 1983).

On the other hand, wolves will take advantage of easy travel routes, such as frozen lakes and shorelines, through prey-free areas (Stenlund 1955; Mech 1966b; Jordan et al.

1967; Peterson 1977) to get to where the prey is. In certain areas of Europe where there are no large prey, wolves hide in sterile, isolated habitat types such as mountain-sides by day, then venture around villages and garbage dumps at night (Zimen and Boitani 1979).

Spatial Characteristics of Travel

The winter travels of wolves whose routes have been mapped (Burkholder 1959; Mech 1966b; Jordan et al. 1967; Pimlott et al. 1969; Haber 1977; Peterson 1977; Jedrzejewski et al. 2001) show three characteristics: long, linear routes, rather than, for example, zigzagging; repeated use of some routes; and a tendency to cover their territory extensively in short periods. That is, instead of searching one end of their territory thoroughly before moving on, the wolves tended to travel linearly from one end of their territory to the other. This was also true of the summer travels of wolves on the arctic tundra (Mech 1988a 1995c).

The extensive, rather than intensive, nature of wolf travel can be seen most dramatically on Isle Royale, where wolves follow the shoreline, trails, ridges, and strings of lakes and bays along the narrow lay of the island (Mech 1966b; Jordan et al. 1967; Peterson 1977). They could have cut across the island instead, but this would have made travel more difficult. Cutting across the island might have exposed more prey to them, however, for they would have had access to prey on both sides of their travel routes, rather than just one.

Even in the SNF on the mainland, wolves travel long strings of frozen lakes and rivers rather than cutting overland (Stenlund 1955; Mech and Frenzel 1971a). They might choose these routes because of the relative ease of travel, but if wolves travel primarily to find prey, and it is faster to find prey by traveling overland, then there may be some other reason why wolves travel linearly. Furthermore, on the arctic tundra during the snow-free summer, wolves also traveled linearly (Mech 1988a, 1995c). Traveling extensively instead of zigzagging over a smaller area would further territorial maintenance, and would add surprise as an advantage in hunting (Mech et al. 1998).

Rotational Use of Territory

Evidence is emerging that wolves may not revisit specific herds of prey for several days after a previous visit. This behavior might serve to reduce the prey's vigilance and

perhaps increase the wolves' chance of catching them off guard (Mech et al. 1998, 105).

Indications of such movement patterns were apparent in travel data presented by Burkholder (1959) and Mech (1966b, 55–57), and possibly Haber (1977). Weaver (1994), however, quantified this behavior by measuring times between visits to individual prey herds. His study pack did not revisit a given elk herd until 12–16 days later, and did not revisit the same bighorn sheep until 36–37 days later. Wolf packs in Poland tended to visit any given area about every 6 days on average (Jedrzejewski et al. 2001).

Trappers' lore and common sense suggest that wolves (and other species) tend to use the same routes repeatedly throughout their lives, and that even after an absence of wolves, new wolves should use the same landscape features. Neither lifelong use nor interrupted sequential use has been documented, however.

Extraordinary Pack Movements

There are a couple of cases of pack movements that are rare exceptions to the patterns described above. Little is known about these movements except their rarity. The first such case was documented in interior Alaska and involved a pack of ten animals that was aerially tracked in the snow for 45 days. This pack covered an area of approximately 128 km (77 mi) by about 72 km (43 mi) (Burkholder 1959). Because these wolves were not radio-collared, nothing is known of where they lived before or after they were tracked. Thus it is not clear whether this was a pack that possessed an extra-large territory, or whether they were more or less nomadic during the study and settled down only if pups were born.

When this information was published, it was not known just how unusual such wide-ranging travels were, for no wolves had yet been radio-tracked. Since then, some two hundred packs have been radio-tracked in Alaska and the adjacent Yukon alone (Stephenson et al. 1995), and many others have been tracked in Canada and elsewhere. Only one other case of such widespread pack movements has been recorded.

This case involved the Little Bear pack, which was radio-tracked from 1988 to 1992 in Denali National Park (Mech et al. 1998). In fall 1991, this pack numbered twenty-three (including at least eleven pups), but it then split during the winter of 1991–1992. In May 1992, a group of eleven wolves, including three radio-collared adults, left and moved some 250 km (150 mi) to the

southwest, where they eventually settled (Mech et al. 1998). They had not produced pups before they left, and it is unclear whether they produced any after they settled. This appeared to be a mass emigration. A shorter emigration was seen in Minnesota (Fuller 1989b). Nothing more is known about wolf emigration, but presumably it takes place in response to a food shortage.

It should be clear from the above discussion that the wolf has a highly adaptable social ecology that is flexible enough to contend with a wide variety of living conditions. Where food is small and scattered, offspring dis-

perse early, and packs are small. Where prey is much larger than the wolf itself, breeding pairs bring young from two or three litters with them as they travel and hunt, and packs are much larger. Changes in prey availability are met with changes in dispersal rates. Similar dynamics affect a population's social structure, with longer-term prey fluctuations translated into adjustments in the territorial mosaic. Such social fluctuations help wolves contend with the ever-changing nature of their dynamic economy—a live prey base that is itself subject to the vagaries of more basic environmental perturbations.