

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USGS Northern Prairie Wildlife Research Center

Wildlife Damage Management, Internet Center for

2003

Wolf-Prey Relations

L. David Mech

USGS Northern Prairie Wildlife Research Center, david_mech@usgs.gov

Rolf O. Peterson

Michigan Technological University

Follow this and additional works at: <https://digitalcommons.unl.edu/usgsnpwrc>



Part of the [Animal Sciences Commons](#), [Behavior and Ethology Commons](#), [Biodiversity Commons](#), [Environmental Policy Commons](#), [Recreation, Parks and Tourism Administration Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

Mech, L. David and Peterson, Rolf O., "Wolf-Prey Relations" (2003). *USGS Northern Prairie Wildlife Research Center*. 321.
<https://digitalcommons.unl.edu/usgsnpwrc/321>

This Article is brought to you for free and open access by the Wildlife Damage Management, Internet Center for at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USGS Northern Prairie Wildlife Research Center by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

5

Wolf-Prey Relations

*L. David Mech and
Rolf O. Peterson*

L. David Mech, US Geological Survey, Jamestown, ND
Rolf O. Peterson, Michigan Technological University, Houghton, MI

AS I (L. D. MECH) watched from a small ski plane while fifteen wolves surrounded a moose on snowy Isle Royale, I had no idea this encounter would typify observations I would make during 40 more years of studying wolf-prey interactions.

My usual routine while observing wolves hunting was to have my pilot keep circling broadly over the scene so I could watch the wolves' attacks without disturbing any of the animals. Only this time there was no attack. The moose held the wolves at bay for about 5 minutes (fig. 5.1), and then the pack left.

From this observation and many others of wolves hunting moose, deer, caribou, muskoxen, bison, elk, and even arctic hares, we have come to view the wolf as a highly discerning hunter, a predator that can quickly judge the cost/benefit ratio of attacking its prey. A successful attack, and the wolf can feed for days. One miscalculation, however, and the animal could be badly injured or killed. Thus wolves generally kill prey that, while not always on their last legs, tend to be less fit than their conspecifics and thus closer to death. The moose that the fifteen wolves surrounded had not been in this category, so when the wolves realized it, they gave up. That is most often the case when wolves hunt.

Throughout the wolf's range (most of the Northern Hemisphere; see Boitani, chap. 13 in this volume), ungulates are the animal's main prey (see Peterson and Ciucci, chap. 4 in this volume). Ordinarily, ungulate populations include both a secure segment of healthy prime animals and a variety of more vulnerable or less fit individuals: old animals; newborn, weak, diseased, injured, or debilitated animals; and juveniles lacking the strength,

experience, and vigor of adults. Prey populations sustain themselves by the reproduction and survival of their vigorous members. Wolves coexist with their prey by exploiting the less fit individuals. This means that most hunts by wolves are unsuccessful, that wolves must travel widely to scan the herds for vulnerable individuals, and that these carnivores must tolerate a feast-or-famine existence (see Peterson and Ciucci, chap. 4, and Kreeger, chap. 7 in this volume).

When environmental conditions change, the relationship between wolves and prey shifts: conditions favorable to prey hamper wolf welfare; conditions unfavorable to prey foster it. With their high reproductive and dispersal potential (see Mech and Boitani, chap. 1, and Fuller et al., chap. 6 in this volume), wolves can readily adjust to changes in proportions of vulnerable prey. The result is that, under average prey conditions, wolf populations generally survive at moderate, lingering levels. All the while, they remain poised to exploit vulnerable prey surpluses, expand, and disseminate dispersers far and wide to colonize new areas (Mech et al. 1998).

Prey and Their Defenses

The dependence of wolves on ungulates implies that the entire original range of the wolf around the world must have been occupied ungulates, and that is indeed the case. Although ungulates vary considerably and may occupy highly specialized habitats, some representative of this large group of hoofed mammals lives almost everywhere throughout wolf range, from pronghorns on the



FIGURE 5.1. Healthy prime-aged moose can withstand wolves. These wolves left after 5 minutes.

prairie to mountain goats on the craggiest cliffs. And the primary predator on all of them is the wolf.

Each ungulate species is superbly and uniquely adapted to survive wolf predation. Most possess several defensive traits, while some depend on one or a few (table 5.1). In no case can a wolf merely walk up and kill a healthy ungulate that is more than a few days old.

All but a few ungulate species are highly alert and responsive to sight, smell, and sound (see table 5.1). The degree of such vigilance is affected by several factors (table 5.2). This fine-tuning of vigilance serves ungulates well in allowing them to feed relentlessly while still being able to suddenly choose their course of escape or defense should wolves threaten. With deer (Mech 1984), sheep (Murie 1944), goats, pronghorn, and even hares (L. D. Mech, unpublished data), all of whose other main defense is flight, either away from the predators or to safer terrain, alertness could make the difference. Furthermore, after wolves have hunted an area, local prey increase their vigilance (Huggard 1993b; Laundré et al. 2001; K. E. Kunkel et al., unpublished data). Deer, beavers, and probably most other prey species can even distinguish the odor of predator urine or feces (Muller-Schwarze 1972; Steinberg 1977; Ozoga and Verme 1986; Swihart et al. 1991; Smith et al. 1994), and probably use this ability to avoid their enemies (Adams, Dale, and Mech 1995).

Clearly speed combined with vigilance is an important defensive factor for smaller prey. R. O. Peterson (unpublished data) measured the speed of an arctic hare at 60 km (36 mi)/hr. White-tailed deer can run at 56 km (34 mi)/hr or more (Newsom 1926, 174, cited in Taylor 1956) and can leap hurdles as high as 2.4 m (Sauer 1984); these abilities facilitate their flight through the thick forested areas they often frequent and through deep snow (Mech and Frenzel 1971a). Although most chases of deer by wolves appear to be relatively short (Mech 1984), deer do possess the endurance to flee for 20 km (12 mi) or more (Mech and Korb 1978). Other relatively small ungulates such as sheep and goats combine alertness and speed with ability to outmaneuver wolves around steep, dangerous terrain, and thereby manage to evade wolves. When on level ground, these animals are almost defenseless (Murie 1944).

In addition to these obvious types of defense, prey animals use a variety of more subtle defensive and risk-reducing behaviors (Lima and Dill 1990); the precise manner in which many of these behaviors work is still unknown (see table 5.1). White-tailed deer, for example, flag their tails in response to disturbance. The most recent explanation for this behavior is that it signals the predator that its presence is known and that pursuit is therefore useless (Caro et al. 1995).

At the other end of the size spectrum, prey such as

TABLE 5.1. Antipredator characteristics and behavior of wolf prey species

Trait/behavior	Species	Reference
<i>Physical traits</i>		
Size	Moose	Mech 1966b
	Bison	Carbyn et al. 1993
	Muskoxen	Gray 1987
Weapons		
Antlers/horns	Male ungulates	Nelson and Mech 1981
	Some females	See text
Hooves	All ungulates	See text
Cryptic coloration	Most ungulate young	Lent 1974
Speed/agility	Pronghorn	Kitchen 1974
	Hares	Mech, unpublished data
	Blackbuck	Jhala 1993
Lack of scent	Deer neonates	Severinghaus and Cheatum 1956
<i>Behavior</i>		
Birth synchrony	Most ungulates	Estes 1966; Rutberg 1987; Ims 1990; Adams and Dale 1998b
Hiding	Deer neonates	Walther 1961; Lent 1974; Carl and Robbins 1988
	Pronghorn neonates	Lent 1974; Carl and Robbins 1988
Following	Caribou neonates	Walther 1961; Lent 1974
	Goat neonates	Lent 1974
	Sheep neonates	Lent 1974
	Moose neonates	Lent 1974
Aggressiveness	All ungulates	See text
Grouping	Caribou	Bergerud et al. 1984
	Elk	Darling 1937; Hebblewhite and Pletscher 2002
	Muskoxen	Gray 1987; Heard 1992
	Bison	Carbyn et al. 1993
	Deer (winter)	Nelson and Mech 1981
	Pronghorn	Kitchen 1974; Berger 1978
	Sheep	Berger 1978
	Goats	Holroyd 1967
	Hares	Mech, unpublished data
	All species	Dehn 1990; Laundré et al. 2001
	Deer	Mech 1966a
	Deer	Schaller 1967; Hirth and McCullough 1977; LaGory 1987
	Sheep	Berger 1978
	Deer	Smythe 1970, 1977; Bildstein 1983; LaGory 1986; Caro et al. 1995
	Elk	Guthrie 1971
Visual signals	Sheep	Berger 1978
	Muskoxen	Gray 1987
	Arctic hares	Mech, unpublished data

(continued)

TABLE 5.1 (continued)

Trait/behavior	Species	Reference
<i>Landscape use</i>		
Migration	Caribou	Banfield 1954
	Deer	Nelson and Mech 1981
	Elk	Schaefer 2000
	General	Fryxell et al. 1988
Nomadism	Caribou	Bergerud et al. 1984
	Muskoxen	Gray 1987
	Bison	Roe 1951
	Saiga	Bannikov et al. 1967
Spacing		
Away	Caribou	Bergerud et al. 1984; Ferguson et al. 1988; Adams, Dale, and Mech 1995
	Deer	Hoskinson and Mech 1976; Mech 1977a,d; Nelson and Mech 1981
Out	Moose	Edwards 1983; Stephens and Peterson 1984
	Deer	Nelson and Mech 1981
	Moose	Mech et al. 1998
	Caribou	Bergerud et al. 1984
Escape features		
Water	Deer	Nelson and Mech 1981
	Moose	Peterson 1955; Mech 1966b
	Caribou	Crisler 1956
	Elk	Cowan 1947; Carbyn 1974
	Beavers	Mech 1970
Steepness	Sheep	Murie 1944; Sumanik 1987
	Goats	Rideout 1978; Fox and Streveler 1986
Shorelines	Caribou	Bergerud 1985; Stephens and Peterson 1984
Burrows	Wild boar	Grundlach 1968

TABLE 5.2. Factors affecting vigilance in wolf prey

Factor	Reference
Body size	Berger and Cunningham 1988
Herd size	Berger 1978; Lipetz and Bekoff 1982
	LaGory 1987; Berger and Cunningham 1988; Dehn 1990
Position in herd	Lipetz and Bekoff 1982
	Berger and Cunningham 1988
Maternal status	Lipetz and Bekoff 1982; Boving and Post 1997; Berger, Swenson, and Persson 2001
Cover	LaGory 1986, 1987
Degree of predator risk	Boving and Post 1997; Berger, Swenson, and Persson 2001

moose (Mech 1966b; Peterson 1977), bison (Carbyn et al. 1993), horses, muskoxen (Gray 1987; Mech 1988a), elk (Landis 1998), wild boar (Reig 1993), and even domestic cattle depend on their sheer size and aggressiveness for much of their defense. Although individuals of any of these species will flee if they detect wolves from far enough away, they will stand their ground and fight when confronted. They lash out with heavy hooves, and those with horns or antlers wield them well. Even deer hooves and antlers can be deadly weapons, and some deer will stand and fight off wolves (Mech 1984; Nelson and Mech 1994). Wolves have been killed by moose (MacFarlane 1905; Stanwell-Fletcher and Stanwell-Fletcher 1942; Mech and Nelson 1990a; Weaver et al. 1992), muskoxen (Pasitchniak-Arts et al. 1988), and deer (Frijlink 1977; Nelson and Mech 1985; Mech and Nelson 1990a).

The large ungulates are especially aggressive when defending their young. Cow moose are dangerous even to humans when their calves are newborn, and they will battle wolves fiercely to protect their young calves (Mech 1966b; Peterson 1977; Stephenson and Van Ballenberghe 1995). When the calves are several months old, a cow running from wolves remains close to her calves' rear ends (their most vulnerable area) and tries to trample any wolf coming close (Mech 1966b). In one case, a cow moose fended off wolves from her two dead 10-month-old calves for 8 days (Mech et al. 1998).

Muskoxen form a defensive line or ring to protect calves (Hone 1934; Tener 1954; Gray 1987; Mech 1988a). All the oxen press their rumps together in front of their young, and the calves press in close to the rumps of their mothers. Bison react similarly, with calves running to the herd and seeking protection from adults (Carbyn and Trottier 1987, 1988). Both muskoxen and bison, especially calves, are most vulnerable to wolves when running (see Gray 1983, 1987; Mech 1987b, 1988a for muskoxen; Carbyn and Trottier 1988 for bison).

Water as a Defense

One of the defensive techniques that most wolf prey resort to when possible is to run into water (Mech 1970). This tactic may provide the prey with several advantages, and it seems to hinder the wolves. Larger prey can stand in deeper water than a wolf can, so the wolf would have less leverage there. The prey can also stand still in the water, while the wolf and its companions must maneuver around through the water. Long-legged species such as moose probably could wallop a wolf with a hoof while the wolf is forced to swim around it. On the other hand, a swimming wolf has been known to kill a swimming deer (Nelson and Mech 1984).

Another common wolf prey species uses water in a different way to protect itself. By building dams, the beaver surrounds itself and its lodge with water deep enough to provide security from wolves most of the time (Mech 1970). It is vulnerable to wolves primarily when it ventures ashore or on top of the ice to cut food, or when its pond freezes to the bottom and the wolves dig the beavers out of the lodge (Mech 1966b; Peterson 1977). The propensity of wolves to travel on beaver dams, where crossing places used by beavers are quite obvious, suggests that waiting at such points at night when beavers are active would be a successful hunting strategy for wolves.

Safety in Numbers

Another defensive trait of many wolf prey species, small and large alike, is herding (Nelson and Mech 1981; Messier et al. 1988). Prey as diverse as wild boar, elk, muskoxen, saiga antelope, domestic animals, and arctic hares, as well as many others, live in herds, at least during certain seasons. The antipredator benefits of herding are well known (Williams 1966; Hamilton 1971): (1) increased sensory potential (Galton 1871; Dimond and Lazarus 1974), (2) dilution of risk (Nelson and Mech 1981), (3) greater physical defense, (4) increased predator confusion (McCullough 1969), (5) a reduced predator/prey ratio (Brock and Riffenburgh 1960), and (6) an increased foraging/vigilance ratio (Hoogland 1979).

Herding is so beneficial that some species go to great lengths to group together during their most vulnerable season, winter. White-tailed deer, for example, which live solitarily during summer, may migrate 40 km (24 mi) or more to herd, or "yard," on winter range (Nelson and Mech 1981). Elk sometimes join herds of 15,000 or more (Boyd 1978), although sometimes living in small herds reduces their rate of encounter with wolves (Hebblewhite and Pletscher 2002). Muskox herd size increases by 70% in winter, and the higher the wolf density, the higher the herd size (Heard 1992). Moose tend to aggregate in larger groups the farther they are from cover (Molvar and Bowyer 1994), probably because moose use woody vegetation as a tactical defense when attacked by wolves (Geist 1998).

Movements

Migration itself, aside from herding, also tends to reduce predation. Migration (seasonal movement between different ranges) can carry ungulates to more favorable areas away from wolves (Seip 1991) and increase wolf search time. Modeling of African ungulates suggests that migration confers such a strong antipredator benefit that migrants should always outcompete residents (Fryxell et al. 1988). By itself, migration may greatly increase an ungulate's short-term risk (Nelson and Mech 1991), but this fact only further supports the long-term benefit of migration. That migration is a general adaptation to enhance survival is shown by the tendency for cow elk that have calves to migrate farthest to escape deep snow in Yellowstone's Northern Range, both before and after the introduction of wolves in 1995 (Schaefer 2000). In some areas, elk migrate 64 km (38 mi) or more (Boyd 1978).

An increase in search time is also an advantage of the nomadism (constant movement over a large area) that several ungulates practice (see table 5.1). Mech was continually impressed with the difficulty of finding nomadic caribou every time he searched by helicopter for the Denali herd in Alaska. Despite the advantages of speed, broad visibility, and a general knowledge of past areas the caribou had frequented, it often took him hours to find them. A related type of wolf avoidance was documented for a bison herd of about ninety that fled 81.5 km (50 mi) during the 24 hours after wolves killed a calf in the herd (Carbyn 1997). L. D. Mech (unpublished data) has noticed that muskox herds also tend to disappear from a region after wolves have killed one.

Spacing

Caribou and other ungulates (Kunkel and Pletscher 2000) also space themselves in other ways that tend to thwart wolves. "Spacing out" (Ivlev 1961) is the tendency of prey to disperse themselves widely within their populations, which helps maximize wolf search time (e.g., deer in the Superior National Forest: Nelson and Mech 1981). A similar advantage is gained by the "spacing away" of caribou cows, the tendency to calve on steep mountain ridges, in extensive spruce swamps, or in other areas far from wolf travel routes such as rivers and from other potential wolf food sources ("apparent competition": Holt 1977) such as moose, which concentrate in lower areas with better nutrition (Bergerud et al. 1984, 1990; Bergerud 1985; Edmonds 1988; Bergerud and Page 1987).

Similarly, the spacing of calving caribou herds away from wolf denning areas or year-round wolf territories also increases wolf search and travel times, thus reducing predation risk (Bergerud and Page 1987; but cf. Nelson and Mech 2000). The Denali herd used this tactic to avoid any increase in wolf predation risk even when the wolf population doubled (Adams, Singer, and Dale 1995). A more dramatic example is the extensive spring migration of barren-ground caribou, which travel hundreds of kilometers from their winter range to calving grounds where wolf numbers are minimal (Bergerud and Page 1987 and references therein). By frequenting islands, peninsulas, shorelines, and other areas where exposure to approaching predators is minimized, prey reduce their chances of encounters with wolves (Edwards 1983; Stephens and Peterson 1984; Bergerud 1985; Ferguson et al. 1988).

These areas, along with mountaintops and extensive habitats such as spruce swamps that few prey, and thus few predators, regularly frequent, are especially important as birthing areas (Skoog 1968; Bergerud et al. 1984, 1990; Bergerud 1985; Bergerud and Page 1987; Adams, Dale, and Mech 1995). If using such areas improves the chances of a newborn's survival for just its first few days when it is most vulnerable, that might make the difference between whether the animal lives out a full life or not.

Wolf Territory Buffer Zones

A specialized type of spacing away involves wolf pack territory buffer zones, or overlap zones along the edges of territories (see Mech and Boitani, chap. 1 in this volume). During a drastic deer decline, wolves in the Superior National Forest eliminated deer first from the cores of their territories and only last from the edges. Based on this observation, Mech (1977a,d) proposed the existence of a buffer zone, or a "no-man's land," thought to be from 2 (Peters and Mech 1975b) to possibly 6 km wide (Mech 1994a). He felt that the reason deer survived longer along these territory edges might be that neighboring packs felt insecure in the buffer zone so spent less time there, minimizing hunting pressure on the deer there. In both summer and winter, deer were more abundant in buffer zones than in territory cores (Hoskinson and Mech 1976; Mech 1977a,d; Rogers et al. 1980; Nelson and Mech 1981). Similar wolf-deer relationships were observed in northwestern Minnesota (Fritts and Mech 1981) and on Vancouver Island (Hebert et al. 1982; Hatter 1984). Furthermore, theoreticians have found mathematical support for the buffer zone as a prey refuge (Lewis and Murray 1993), and others have described similar prey-rich zones between warring Indian tribes (Hickerson 1965, 1970; Martin and Szuter 1999). Carbyn (1983b) did not find disproportionate use by elk of pack boundary edges in Riding Mountain National Park.

"Swamping"

Another antipredator strategy pervasive among wolf prey species that helps promote survival of their young is the tendency toward synchronous births (Estes 1966; Wilson 1975). This phenomenon tends to "swamp" wolves with a short burst of vulnerable individuals of a given species. While wolves are occupied preying on some individuals, the others grow quickly and become

less vulnerable by the day. For example, about 85% of caribou calves in Denali National Park are born within a 2-week period (Adams and Dale 1998b). During years of favorable weather, almost all the wolf predation on calves takes place during the calves' first 2 weeks of life (Adams, Singer, and Dale 1995). Similarly, white-tailed deer and arctic hares are born over a short period and tend to be vulnerable to wolves primarily during their first few weeks of life (Kunkel and Mech 1994 for deer; L. D. Mech, unpublished data, for hares). Because neonates of most ungulates are so vulnerable, but develop so quickly, it seems reasonable that swamping in some form helps minimize wolf predation on them as well.

Hunting Success

The many effective antipredator traits and strategies of most prey ensure that most hunts by wolves are unsuccessful (Mech 1970). Moreover, the actual hunting success of any predator varies considerably and depends

greatly on many circumstances, such as season, time of day, weather, and terrain; predator experience; prey species, numbers, age, sex, associates, and vulnerability; past and immediate prey history; and no doubt many other factors. Furthermore, subtle factors, such as prey odor, prey behavior, and recent exposure of prey to attacks, may play important roles in the outcome of wolf-prey encounters (Haber 1977; Carbyn et al. 1993).

Measurements of wolf hunting success have been made primarily in winter, when hunting success for most large prey species is probably maximal because their vulnerability is greatest then (see below). In addition, the fact that many of the wolf's prey species live in herds complicates determinations of success. If wolves kill one elk in a single attack on a herd, but try to catch three of them, is their success rate 100% or 33%? Thus we have only a glimpse of the total picture. This glimpse shows both the relatively low success rate and its variation (10–49% based on number of hunts and 1–56% based on number of prey attacked) (table 5.3).

TABLE 5.3. Wolf hunting success rates based on number of hunts (encounters involving groups of prey) and on number of individual prey animals

Prey	Location	Number		Kills	% success based on		Reference
		Hunts	Individuals		Hunts	Individuals	
<i>Winter^a</i>							
Moose	Isle Royale, MI	—	77	6–7 ^b	—	8–9 ^b	Mech 1966b
Moose	Isle Royale, MI	—	38	1	—	3	Peterson 1977
Moose	Kenai, AK	—	38	2	—	5	Peterson, Woolington, and Bailey 1984
Moose	Denali, AK	—	389	23	—	6 ^c	Haber 1977
Moose	Denali, AK	37	53	7–14 ^b	19–38	13–26 ^b	Mech et al. 1998
Deer	Ontario	—	35	16	—	46 ^e	Kolenosky 1972
Deer	Minnesota	—	60	12	—	20	Nelson and Mech 1993
Caribou	Denali, AK	—	16	9	—	56 ^c	Haber 1977
Caribou	Denali, AK	26	303	4 ^d	15	1	Mech et al. 1998
Dall sheep	Denali, AK	—	100	24	—	24 ^c	Haber 1977
Dall sheep	Denali, AK	18	186	6	33	3	Mech et al. 1998
Bison	Alberta	31	—	3	10	—	Carbyn et al. 1993, table 46
Elk	Yellowstone, WY	102	1,532	21	21	1	Mech et al. 2001
<i>Summer</i>							
Bison	Alberta	86	—	28	33	—	Carbyn et al. 1993, table 48
Caribou	Denali, AK	110	1,934	54	49	3 ^c	Haber 1977
Dall sheep	Denali, AK	14	108	4	29	4 ^c	Haber 1977

^aResults from Mech et al. 1998 include a few instances from spring, summer, and fall.

^bLarger figures include wounded animals that may have died later.

^cResults from Haber 1977 should be considered minimum estimates because he included prey that he believed the wolves "tested" from distances of "several hundred feet or more" (Haber 1977, 381).

^dIncludes two newborn calves in May.

^eProbably biased upward because it was based on ground tracking where likelihood of interpreting kills is much greater than for failures (Kolenosky 1972).

One factor that might influence wolf hunting success rate is motivation based on time since last kill. However, wolves sometimes show interest in attacking prey within minutes of leaving a kill (Mech 1966b), or stop feeding on fresh kills to take advantage of new opportunities to catch prey (L. D. Mech, unpublished data). Thus it is not surprising that wolves seem to show no more intensity in attacking prey several days after feeding than just a day after.

Effects of Snow and Other Weather

Because wolves tend to kill prey that are vulnerable, and because prey vulnerability is greatly affected by weather conditions, weather is important to wolf-prey relations. The most significant weather factor is snow conditions, including snow depth, density, duration, and hardness.

Snow affects prey animals primarily by hindering their movements, including foraging and escape from wolves. The effect of snow on prey escape is mechanical: the deeper and denser the snow, the harder it is for prey to run through it. Most prey probably have a heavier foot loading than do wolves, so they would sink deeper and be hindered more than wolves. Estimates for foot loading in deer, for example, range from 211 g/cm² (Mech et al. 1971) to 431–1,124 g/cm² (Kelsall 1969), whereas for wolves, the estimate is about 103 g/cm² (Foromozov 1946). Ungulates are usually much heavier than wolves and possess hard hooves that puncture snow much more easily than the spreading, webbed toes of a wolf foot. This difference can tilt the balance toward wolves during predation attempts on animals from the size of deer (Mech et al. 1971) to bison (D. R. MacNulty, personal communication).

The condition of snow changes daily, even hourly, and wolves and their prey are very sensitive to subtle changes that might work to their advantage or disadvantage. R. Peterson (personal observation) has seen packs of wolves sleep through late afternoon and early evening during midwinter thaws, apparently waiting for the crusted snow that will follow when the temperature drops at night. During daily tracking of a pack of five wolves in upper Michigan during a 3-month period, B. Huntzinger (personal communication) documented three cases of the pack killing five to ten deer overnight; during two of these instances the kills were made during heavy blizzards, and in the third case wolves took advantage of a strong snow crust that supported them, but not the deer.

In addition to the acute effect of hindering prey escape, deep snow has a longer, more pervasive effect on prey nutrition. Snow resistance reduces foraging profitability for ungulates and causes them to lose weight over the winter, the amount depending on snow depth and density and duration of cover. During severe winters, prey often starve. The combination of reduced nutrition and poor escape conditions for prey can result in a bonanza for wolves (Pimlott et al. 1969; Mech et al. 1971, 1998, 2001; Peterson and Allen 1974; Mech and Karns 1977; Peterson 1977; Nelson and Mech 1986c).

However, severe snow conditions can also have indirect effects on prey animals that predispose them to wolf predation. These take the form of intergenerational effects and cumulative effects. Intergenerational effects result from the fact that ungulates are gravid over winter. Thus undernutrition or malnutrition caused by deep snow can affect fetal development and viability (Verme 1962, 1963), resulting in offspring with increased vulnerability to wolf predation (Peterson and Allen 1974; Mech and Karns 1977; Peterson 1977; Mech, Nelson, and McRoberts 1991; Mech et al. 1998). This intergenerational effect can even persist for a second generation. That is, animals with poorly nourished grandmothers can be more vulnerable to wolf predation even if their mothers were well nourished (Mech, Nelson, and McRoberts 1991; also see below).

The cumulative effects of snow conditions on prey vulnerability operate across winters. Ungulates must replenish their nutritional condition during the snow-free period each year. Thus if the replenishment period is too short, or if an animal reaches that period in too poor a condition, that creature may be vulnerable the next winter (Mech 2000d). If it survives, its condition may worsen, especially if the following winter is also severe or prolonged. In this manner, a series of severe winters can cumulatively reduce an animal's condition and increase its vulnerability (Mech, McRoberts et al. 1987; McRoberts et al. 1995; cf. Messier 1991, 1995a).

These same principles operate in the opposite direction if winters are mild and snow depth low or snow cover duration short. The result is prey in better condition and with lower vulnerability.

Although the effects of snow conditions on wolf-prey relations are the best-studied weather effects, drought and probably several other extreme conditions that affect prey nutrition no doubt similarly influence wolf-prey relations. For example, warm and dry weather during spring leads to heavy infestations of winter ticks

(*Dermacentor albipictus*) the following winter in North American moose, which cause direct mortality from starvation and probably make the moose more vulnerable to hunting wolves (DelGiudice, Peterson, and Seal 1991; DelGiudice et al. 1997).

The effects of weather, especially snow, so pervade wolf-prey relations that some workers believe that they actually drive wolf-prey systems (Mech and Karns 1977; Mech 1990a; Mech et al. 1998; Post et al. 1999). When snow conditions are severe over a period of years, they reduce prey survival and productivity, and wolves increase for a few years, whereas during periods of mild winters, the opposite happens. This bottom-up interpretation of driving factors may seem to conflict with a top-down interpretation (McLaren and Peterson 1994). However, ecosystems are complex and dynamic, with multiple food chains, so they can include both bottom-up and top-down influences (see Sidebar).

The Role of Tradition

Captive-raised wolves with no experience can hunt and kill wild prey and survive for years when released into the wild (Klein 1995) just as dogs, cats, and other species can hunt and kill instinctively. Captive-reared Mexican wolves (*Canis lupus baileyi*) reintroduced into Arizona in the spring of 1998 began killing elk within about 3 weeks of release (D. R. Parsons et al., personal communication). The wolves translocated from Canada to Yellowstone began killing elk within days after their release, despite no tradition of hunting in the area.

Nevertheless, it seems reasonable to suggest that naturally raised wolves gain a keen knowledge of the prey in their territory and that they develop habits, traditions, and search patterns that increase their hunting efficiency. Under good conditions (for example, in the case of the wolves reintroduced in Yellowstone) such an advantage may not be crucial, but perhaps with fewer or less vulnerable prey, it might make some difference.

This supposition has been extended to great lengths with the contention that tradition is critical to wolves and that packs are inbred groups that maintain long traditions of hunting routes and habits (Haber 1996). However, as indicated by Wayne and Vilà in chapter 8 in this volume, wolves generally outbreed (D. Smith et al. 1997), and the turnover of individuals in packs is high (Mech et al. 1998), so this extreme degree of reliance on tradition seems highly unlikely. Furthermore, the facts that dispersing wolves readily colonize new areas and prosper

(Rothman and Mech 1979; Fritts and Mech 1981; Ream et al. 1991; Wydeven et al. 1995; Wabakken et al. 2001) and that populations quickly recover following wolf control (Ballard et al. 1987; Potvin et al. 1992; Hayes and Harestad 2000a) demonstrate that hunting traditions are far from critical to wolf functioning under most conditions. The constant variation of wolf prey vulnerability (Mech, Meier et al. 1995; Mech et al. 1998) may force wolves to be flexible enough to deal with the conditions of the moment rather than relying heavily on traditions.

The above overview of wolf-prey relations does not necessarily apply to wolf interactions with domestic prey. Domestication has left some prey, such as sheep, defenseless, and the ways in which humans restrain domestic animals—for instance, in wide-open, fenced fields—often makes them more vulnerable to predation. Thus wolf predation on domestic animals does not necessarily fit generalizations based on wild prey.

Characteristics of Wolf Predation

Prey Species Preferences

Do wolves prefer certain prey species? This is an interesting question and one not easily answered. Generally wolves eat whatever meat is available, including carrion and garbage (see Peterson and Ciucci, chap. 4 in this volume). There is probably not one potential prey species in wolf range that wolves have not killed. Furthermore, wolves in the ranges of several prey species kill them all. Single packs in Denali National Park, for example, kill moose, caribou, and Dall sheep, as well as many smaller species (Murie 1944; Haber 1977; Mech et al. 1998). The question can be broken down into two parts: First, do individual wolves or packs prefer to prey on certain species if given choices? Second, how readily do wolves that are accustomed to preying on certain species learn to prey on others, and under what circumstances will they switch prey?

Several observations spawn these questions. Cowan (1947) concluded that in the Canadian Rockies, wolves tended to forsake mountain sheep and goats for elk, deer, and moose. Carbyn (1974, 173) stated that, in the same area Cowan studied, “elk calves and mule deer are preferred prey, followed by adult elk, moose, sheep, small mammals, caribou and goat.” In Riding Mountain National Park, Carbyn (1983c) found that wolves killed elk disproportionately to moose. Fritts and Mech (1981)

noted that several wolf packs living among farms continued preying on wild prey and did not kill domestic animals. Potvin et al. (1988) learned that even when deer were scarce, wolves concentrated on them during winter despite the presence of moose. On the other hand, in Minnesota, wolf packs preying primarily on deer sometimes killed moose (Mech 1977a; L. D. Mech, unpublished data). Dale et al. (1995) recorded wolves preying primarily on caribou even though moose were more abundant. Kunkel et al. (in press) found that although wolves tended to hunt during winter in deer concentration areas, they killed disproportionately more elk and moose.

Speculating about this subject, Mech (1970, 205) wrote the following: "No doubt wolves in each local area become very skilled at hunting prey on which they specialize. But it is also possible that the same animals might be inept at hunting species they have never seen. It would be extremely interesting to take a pack that is accustomed to killing deer, for instance, and move it to an area where caribou and moose are the only prey available. Possibly such a pack would be at so great a disadvantage that it would fail to survive."

That experiment still has not been done; however, similar tests have been performed. Captive-reared wolves that had never killed any prey were released on Coronation Island, Alaska, and just about exterminated the deer there (Klein 1995). Similarly, captive-raised red wolves learned to kill deer and smaller prey upon release (see Phillips et al., chap. 11 in this volume). Captive-reared Mexican wolves began killing elk within 3 weeks of release, as we saw above. Bison-naïve wolves reintroduced into Yellowstone National Park learned to kill bison within 21 days to 25 months after release (Smith et al. 2000). This evidence weakens the notion that individual wolves cannot learn to hunt and kill prey with which they have never had experience.

But this evidence still does not show that wolves highly experienced with one kind of prey can readily hunt and kill others. Although we strongly suspect they can, it is worth considering how to explain the observations of apparent prey preferences mentioned above. Those observations do not constitute definitive evidence for prey preferences because no study has compared the vulnerabilities of several prey species in a given area and thus ruled out the possibility that an apparent species preference was anything more than a temporary differential vulnerability.

Huggard (1993b) and Weaver (1994) illustrated some of the complexities involved in analyzing prey selection patterns by recording locations of deer and elk as well as the travel patterns and success rates of hunting wolves. If deer scattered across the landscape could not be located or killed, it became profitable to go to predictable elk locations, even when groups of elk were fewer.

While elements of learning, tradition, and actual preference may be involved in apparent prey species preferences, the most likely explanation for these patterns involves a combination of capture efficiency and profitability relative to risk, which boils down to prey vulnerability. In other words, we believe that as wolves circulate around their territories and encounter and test prey under constantly changing conditions, they gain information about the relative vulnerability of various types of prey to hunting (including finding, catching, and killing). Through trial and error they end up with whatever prey they can capture. Thus as conditions change, the wolves' prey changes in species, age, sex, and condition. This explains the seasonal and annual variation so apparent in any overview of wolf predation for any given area (Mech et al. 1998). It would also explain the finding that, in the Glacier National Park area, wolves killed disproportionately more elk and moose even though frequenting an area with more deer (Kunkel et al., in press).

Relying on whatever class of prey is currently vulnerable means that lags are inevitable because of the time it takes for wolves to gather the information about changing conditions. With the dramatic burst of vulnerable newborn caribou calves each spring, for example, it takes the wolves about a week to begin utilizing them (Adams, Singer, and Dale 1995).

Detailed analyses have been attempted to try to explain why wolves seem to specialize in killing more of some prey species when others are available (Huggard 1993b; Weaver 1994; Kunkel 1997). However, such studies must assume that equal proportions of each prey species are equally vulnerable at any given time—a critical condition that cannot be demonstrated and probably is rarely true. Therefore, we doubt that a more detailed explanation will be forthcoming than that wolves prey on whatever individuals of whatever species are vulnerable enough for them to kill with the least risk at any given time.

Vulnerability and Prey Selection

As we indicated earlier, wolves tend to kill the less fit prey. Evidence for this contention is considerable (summarized by Mech [1970], Mech et al. [1998], and in table 5.4); the main aspect of this issue that needs further study is the question of when or whether wolves *ever* take prey that are maximally fit. Given that it is almost impossible to gather enough evidence to prove that an animal is fit in every way (Mech 1970, 1996), this question may forever go unanswered. For example, even if a fresh, intact carcass of a wolf-killed animal could be examined, one could not determine enough about the animal's sensory abilities or keenness to draw conclusions about its fitness.

Our reasoning for claiming that wolves are heavily reliant on prey that are in some way defective is as follows (cf. Mech 1970). A complete examination of an animal for any traits that might predispose it to predation would require testing of live prey for various sensory, mental, behavioral, or physiological flaws as well as intact carcasses for detecting any anatomical or pathological conditions. Rarely are enough remains of wolf prey found to

allow anything close to a complete carcass examination; most often the only remains are bones, and even then the complete skeleton is rarely available. However, based on even these partial remains of prey, a wide variety of predisposing conditions have been found (see table 5.4). Regardless of the approach used, including examination of prey before death (Seal et al. 1978; Kunkel and Mech 1994) and comparison of wolf-killed prey with the prey population at large (Pimlott et al. 1969; Mech and Frenzel 1971a), the results consistently indicate that wolves tend to kill less fit prey.

One possible exception to this tendency involves calves or fawns. Because remains of prey less than 6 months old are rarely found, it is usually impossible to determine the condition of such animals. Are they vulnerable just because they are young? Certainly some are debilitated, weaker than others, or otherwise inferior (Kunkel and Mech 1994), but are these the only individuals wolves kill? Or are all young-of-the-year more vulnerable?

The answer probably varies by species or even by year or population. Caribou calves in Denali National Park born after average or mild winters, for example, were

TABLE 5.4. Prey characteristics that may determine vulnerability to wolves

Characteristic	Remarks	Reference
Species	Some indication that in multi-prey systems, certain species may be "preferred" to others, but no definitive evidence (see text)	Cowan 1947; Mech 1966a; Carbyn 1974, 1983b; Potvin et al. 1988; Huggard 1993b; Weaver 1994; Kunkel et al. 1999
Sex	Males killed most often around the rut	Nelson and Mech 1986b; Mech, Meier et al. 1995
Age	Calves and fawns and old animals most often taken	Summarized by Mech (1970) and Mech, Meier et al. (1995)
Nutritional condition	Individuals in poor condition most often taken	Summarized by Mech (1970) and Mech et al. (1998); Seal et al. 1978; Kunkel and Mech 1994; Mech et al. 2001
Weight	Lighter individuals most often taken	Peterson 1977; Kunkel and Mech 1994; Adams, Dale, and Mech; 1995 ^a
Disease	Diseased animals most often taken	Summarized by Mech (1970) and Mech et al. (1998)
Parasites	Hydatid cysts and winter ticks may predispose prey	Summarized by Mech (1970) and Mech et al. (1998)
Injuries, abnormalities	Injured or abnormal individuals most often taken	Summarized by Mech (1970) and Mech et al. (1998); Mech and Frenzel 1971a; Landis 1998
Parental or grandparental condition	Offspring of malnourished mothers or grandmothers most often taken	Peterson 1977; Mech and Karns 1977; Mech, Nelson, and McRoberts 1991
Defensiveness	Aggressive individuals taken less often	Mech 1966b, 1988a; Haber 1977; Peterson 1977; Nelson and Mech 1993; Mech et al. 1998
Parental age	Offspring of older parents taken less often	Mech and McRoberts 1990

^aAdams, Dale, and Mech found a strong inverse relationship between caribou birth weight and wolf-caused mortality among, but not within, years.

rarely killed by wolves after they were about a month old (Adams, Singer, and Dale 1995b), so presumably they were not especially vulnerable as a class. On the other hand, deer and moose young are killed throughout their first year (Mech 1966b; Peterson 1977; Nelson and Mech 1986b), so possibly they are more vulnerable. We believe that probably wolves do kill some normal, healthy young prey that are vulnerable just because they are young, but the proportion of such animals in their total take of young probably varies considerably.

Other possible conditions that might make otherwise fit individuals vulnerable to wolves could include the sudden appearance of a strong crust over deep snow (Peterson and Allen 1974), as might follow a rainstorm in winter. Animals such as Dall sheep may suddenly be caught far away from cliffs (although Murie [1944] believed that this is most apt to happen to sheep in poor condition). Other chance circumstances involving environmental conditions might strongly disadvantage a prey animal.

Some of the conditions that predispose prey to wolf predation are dramatic, such as necrotic jawbones (Murie 1944), lungs filled with tapeworm cysts (Mech 1966b), arthritic joints (Peterson 1977), and depleted fat stores (Mech, Meier et al. 1995). However, others are more subtle, such as abnormal blood composition (Seal et al. 1978; Kunkel and Mech 1994) or even malnourished grandmothers (Mech, Nelson, and McRoberts 1991). While it may seem hard to explain how the nutrition of a deer's grandmother has anything to do with the deer's being predisposed to wolf predation, rats with poorly nourished grandmothers show learning deficits (Bresler et al. 1975), fewer brain cells (Zamenhof et al. 1971), and reduced antibodies (Chandra 1975). Any of these traits could predispose an animal to predation.

From a strictly logical standpoint, wolves could not kill every prey individual they wanted to, for given their high productivity and other characteristics, they would soon end up depleting their prey. The wide variety of antipredator traits that prey have evolved (see table 5.1) prevents this outcome. Thus generally wolves must strive hard in order to capture enough prey to survive.

Through constant striving, however, wolves are able to find and capitalize on the usually small proportion of their prey population that is vulnerable. Because of environmental changes and the natural history of prey, defective individuals are constantly being generated. Aging, accidents, progressing pathologies, birth, competi-

tion for food, and various other natural processes assure that. A high degree of buffering in the form of excellent mobility, fat storage, caching behavior, and variation in productivity, survival, and dispersal rates helps wolves survive most mismatches between their needs and the defensive capabilities of their prey (Mech et al. 1998).

Thus as wolves travel about among their prey, they try to catch whatever they can (fig. 5.2). Each attempt represents a test or trial of sorts (Murie 1944; Mech 1966b; Haber 1977). A parsimonious view of how these tests result in the wolves ending up with the inferior prey individuals is that the process happens mechanically. Prey that are not alert, fleet, strong, or aggressive enough simply end up being killed more often.

On the other hand, there may be more to it. A study using borzoi dogs as surrogates for wolves showed that the dogs actually detected inferior members of prey herds and targeted them (Sokolov et al. 1990). Film footage in real time of two wolves chasing a herd of elk clearly documented the wolves scanning the herd by coursing through it at restrained speeds, targeting an individual with an arthritic knee joint (fig. 5.3), and chasing it through the herd until they caught and killed it (Landis 1998). You could almost hear Charles Darwin cheering, "Yes, Yes!"

Kill Rate

The rate at which wolves kill prey has been measured many times and, as is to be expected, is highly variable. Because both prey size and pack size must influence kill rate, it is useful to express kill rate as biomass per wolf per day. The range runs from 0.5 to 24.8 kg/wolf/day (table 5.5). Given all the vagaries of a wolf's existence (countered by the various buffers discussed above), the only reasonably certain generalization that can be made is that wolves kill enough to sustain themselves.

How much does this amount to? Based on studies of dogs and of captive wolves, Mech (1970) concluded that the basic daily requirement for an active animal would be about 1.4 kg/wolf. Assuming about 7 kg of inedibles such as rumen contents and skull, this would amount to about one 45 kg deer per 27 days, or 13 such deer per year. This figure should be considered the minimal maintenance requirement because it is based on captive wolves that are much less active than wild ones. However, wild wolves will eat far more than this minimal requirement. Captive wolves will consume over 3 kg (7 pounds) of



FIGURE 5.2. Wolves usually try to attack any prey they can. When they are chasing prey, often young-of-the-year are strung out behind the adults.



FIGURE 5.3. Arthritic knee joint of an elk culled from a herd by wolves in Yellowstone. Observers filmed two wolves targeting the limping elk from among its herd and killing it (Landis 1998).

food per day (see Peterson and Ciucci, chap. 4 in this volume), and many of the reported kill rates reflect that (see table 5.5).

There is an interesting difference between kill rates for wolves preying on deer and those for wolves preying on larger species. Generally wolf kill rates for larger prey run about five times those for deer (Schmidt and Mech

1997). The highest kill rate reported for deer-killing wolves is 6.8 kg/wolf/day, whereas for wolves killing larger species, it is 24.8 kg/wolf/day (see table 5.5). While it is true that wolves preying on moose and caribou generally weigh about 40% more than those preying on deer, this difference could not account for the difference in kill rates.

So what does account for it? Conceivably, the kill rates for wolves killing deer are higher than have been measured, perhaps because a wolf pack can clean up a deer kill in a few hours and leave, so the kill goes undetected by researchers checking the wolves periodically by aircraft, the usual method (Fuller 1989b). However, even tracking wolves on the ground in the snow (Kolenosky 1972) yields much lower kill rates for deer than for moose or caribou. Possibly greater scavenging (Promberger 1992; Hayes et al. 2000) or caching (Mech and Adams 1999) around larger prey than was earlier realized explains the difference. However, the question remains unanswered.

Seasonal Variation in Kill Rate

The question of seasonal variation in wolf kill rates has been little studied, but, due to the extreme variation in

TABLE 5.5. Wolf kill rates during winter

Prey	Pack size	N	kg/wolf/day	Reference
White-tailed deer	3	1	4.5	Stenlund 1955
White-tailed deer	5	1	0.6	Mech and Frenzel 1971a
White-tailed deer	8	1	3.7	Kolenosky 1972
White-tailed deer	2–9	4	1.6–3.6	Mech 1977a
White-tailed deer	2–7	20	0.5–6.8	Fritts and Mech 1981
White-tailed deer	1–10	— ^a	2.0 ^b	Fuller 1989b
Moose	15–16	36	4.4–6.0	Mech 1966b
Moose	4	1	1.8	Mech 1977a
Moose	6–11	6	4.1–12.1	Fuller and Keith 1980a
Moose	2–9	8	3.5–19.9	Ballard et al. 1987
Moose	2–17	5	5.5–14.6	Peterson, Woolington, and Bailey 1984
Moose	4–11	5	8.7–24.8	Dale et al. 1994
Moose	2–20	40	7.9 ^b	Hayes et al. 2000
Caribou	2–20	20	2.5 ^b	Hayes et al. 2000
Caribou	4–8	3	5.7–10.2	Ballard et al. 1987
Caribou	2–15	13	8.6–24.8	Dale et al. 1994
Dall sheep	6–13	3	8.7–17.9	Dale et al. 1994
Bison	7–13	8	3.5–7.4	Carbyn et al. 1993
Elk	2–14	106	2.3–22.0	Mech et al. 2001

Note: See also Mech 1970.

^aNot given.

^bMean.

environmental conditions throughout the year, it is reasonable to expect much seasonal variation. Almost all kill rate studies have been conducted during winter, so sparse data are available for summer (see table 5.5, Peterson and Ciucci, chap. 4 in this volume). Furthermore, because all kill rate studies have been conducted in the northern part of the wolf's range, where daylight is short until late winter and spring, most such rates are for late winter and spring. That is also the period when ungulate nutritional condition is poorest and ungulates are most vulnerable. Thus published kill rates no doubt represent maxima for the year.

Only a few studies have sought to compare winter wolf kill rates by month. Although Ballard et al. (1987) did not make monthly comparisons, they did estimate that wolves killed about the same biomass of prey during summer as during winter. Three of the studies that did make monthly comparisons (Mech 1977a; Fritts and Mech 1981; D. W. Smith, unpublished data) showed that, as expected, kill rates peak in February and March. A fourth study (Dale et al. 1995) showed higher rates in March than in November, but indicated that the differences were not statistically significant. However, because the researchers' data consisted of all the kills their packs

made during their study, and were not samples, their packs actually did kill more in March than in November.

Surplus Killing

When prey are vulnerable and abundant, wolves, like other carnivores, kill often and may not completely consume the carcasses, a phenomenon known as "surplus killing" (Kruuk 1972) or "excessive killing" (Carbyn 1983b). The amount of each carcass wolves eat depends on how easy it is to kill prey at the time, but sometimes they leave entire carcasses (Pimlott et al. 1969; Mech and Frenzel 1971a; Peterson and Allen 1974; Bjärvall and Nilsson 1976; Carbyn 1983b; Miller et al. 1985; DelGiudice 1998). Surplus killing of domestic animals lacking normal defenses against wolf predation may not be unusual (Young and Goldman 1944; Bjärvall and Nilsson 1976; Fritts et al. 1992), but it is rare for wolves to kill wild prey in surplus. All cases of surplus killing of wild prey reported for wolves have occurred during a few weeks in late winter or spring when snow was unusually deep. In 30 years of wolf-deer study, Mech observed this phenomenon only twice (Mech and Frenzel 1971a; L. D. Mech, unpublished data), and in forty winters of wolf-

moose studies, it was seen in only three winters (Peterson and Allen 1974; R. O. Peterson, unpublished data). DelGiudice (1998) recorded it during only a few weeks in one of six winters.

Presumably what happens when wolves kill more than they can immediately eat is that they respond normally to a situation that is drastically different than usual—prey are highly vulnerable, rather than being especially hard to catch. Programmed to kill whenever possible because it is rarely possible to kill, wolves automatically take advantage of an unusual opportunity.

This phenomenon has not been thoroughly studied. It has been dubbed “surplus killing” because individual carcasses are not eaten right away, contrary to the wolf’s usual hungry habit. However, it stands to reason that, if scavengers did not consume these carcasses, eventually the wolves would return to them when prey was harder to kill, just as they do to caches (see above) or carrion (see Peterson and Ciucci, chap. 4 in this volume). In fact, a follow-up study supports that notion. In Denali National Park, six wolves killed at least seventeen caribou about 7 February 1991, and of course could not eat them all. By 12 February, however, 30–95% of each carcass had been eaten or cached (Mech et al. 1998); by 16 April, wolves had dug up several of the carcasses and fed on them again.

Number of Prey Killed

Actual numbers of individual prey killed per year cannot accurately be determined because of the lack of kill rate data from non-winter periods. Estimates could be made by projecting from late winter data, but besides almost certainly being overestimates, they would require using a sliding scale to account for the ever-growing fawns and calves that constitute much of the wolf’s diet during summer. Supplementary prey such as beavers, hares, and other small animals taken in summer must also be considered (Jedrzejewski et al. 2002).

Nevertheless, attempts have been made to determine annual kill rates of individual prey, but they remain estimates. For deer, they ranged from 15 to 19 adult-sized deer (or their equivalents) per wolf per year, assuming that other prey constitute another 20% of the diet (Mech 1971; Kolenosky 1972; Fuller 1989b). For moose on Isle Royale, where the only other significant prey are beavers, taken mostly during warm periods, the annual estimate was 3.6 adult moose and 5.3 calves per wolf (Mech

1966b). In south-central Alaska, the year-round estimated kill rate, adjusted for prey type (adult and calf moose and caribou), averaged one kill per 8.3 days for a pack of six wolves (Ballard et al. 1987), or about 7.3 kills per wolf per year. For the Western Arctic caribou herd, where an estimated 55% of wolves’ prey was caribou, some 1,740 wolves were estimated to be killing the equivalent of 28,000 adult cows annually, or 16 per wolf per year (Ballard et al. 1997).

Seasonal Vulnerability of Prey

Because of the extreme variation in size and natural history among ungulates, including differences between mature ungulates and their newborn offspring, the type of prey accessible to wolves varies throughout the year. This is especially true when one considers the need for wolf prey to be vulnerable in order to be accessible. For example, newborn ungulates are generally more vulnerable than adults, as we saw above.

An example of seasonal variation in the vulnerability of various age and sex classes, even of a single species, is the white-tailed deer in northeastern Minnesota (Nelson and Mech 1986b). Throughout the year, fawns are vulnerable as a class, although not every individual is (Kunkel and Mech 1994); during summer, adults are rarely taken, so fawns form most of the wolf’s diet. In fall, adult bucks—occupied with fighting and the rut instead of eating—become vulnerable, and finally during late winter and spring, when pregnant does reach the nadir of their condition (DelGiudice, Mech, and Seal 1991), they become more vulnerable (Nelson and Mech 1986b).

This basic pattern varies among different ungulates and areas, and probably among years (Mech 1966b, 1970; Peterson 1977; Peterson, Woolington, and Bailey 1984; Nelson and Mech 1986b; Ballard et al. 1987, 1997; Carbyn et al. 1993; Mech et al. 1998; Kunkel and Pletscher 1999). However, several generalizations can be made. Young are most vulnerable in their first few weeks and remain relatively vulnerable throughout their first year, except for caribou calves (Adams, Dale, and Mech 1995; Adams, Singer, and Dale 1995). Adult males are most vulnerable immediately before, during, and after the rut, and adult females are most vulnerable in late winter. However, depending on the species, area, and year, some adults may be vulnerable year around. In the multi-prey systems of Denali (Mech et al. 1998) and Glacier (Kunkel

and Pletscher 1999; Kunkel et al. 1999) National Parks, various ages and sexes of several ungulate species form different proportions of the wolf's diet during different seasons.

Influences of Wolves on Prey Numbers

Do wolves control the density of their prey, or does wolf predation merely substitute for other mortality? Probably no question has dogged wolf research more, or generated more disagreement among biologists. The influence of wolf predation on prey populations has been a subject of public controversy and scientific debate for decades. How is it possible that wolves introduced to Coronation Island, a small island in southeastern Alaska, almost wiped out the resident black-tailed deer (Klein 1995), yet on Isle Royale wolves coexist with the world's highest density of moose (Peterson et al. 1998)? Can both case studies be understood under a single scientific umbrella? Do they tell us anything useful about wolf predation in mainland systems? Since Mech's (1970) review, there has been a wealth of fieldwork on this subject, as well as much effort to place wolf predation in the context of general ecological theory.

As the complexity and unique features of real-world ecosystems have become more evident, it has also become clear that simple platitudes about whether or not wolves control prey populations are naive (Mech 1970). Under some circumstances, wolves can dramatically reduce, even locally extirpate, some prey species (Mech and Karns 1977). At other times, wolf predation may only compensate for other mortality that takes over in the absence of wolves (Ballard et al. 1987).

Important determinants of wolf-prey relationships include whether or not multiple prey species or other predators (especially humans and bears) are influential in a system, the relative densities of wolves and prey, the responses of wolf and prey populations to prey density, and the effects of environmental influences such as winter severity and diseases on both wolves and prey. All of these factors may affect the rate of increase for prey, the number of wolves present, and the kill rate of prey by wolves.

To discuss this subject, it is first necessary to distinguish among the many terms used to describe the effects of wolf predation. The alleged "control" of prey populations by predators, for example, might be interpreted in at least six ways, depending on the definition used (Tay-

lor 1984). Several recent reviews have used definitions by Sinclair (1989), who proposed that "limiting" factors include all mortality factors that operate in a prey population, and that "regulating" factors are those that act in concert with prey density (i.e., are density-dependent) to maintain prey populations at equilibrium, or within a usual range. Density-dependent mortality, for example, would be proportionately higher when a population is above an equilibrium than below it, while reproduction would follow an opposite trend. The result of such relationships would be a strong tendency for a prey population to stabilize.

While all populations are limited, not all are regulated. Similarly, all regulating factors are limiting factors, but not all limiting factors are regulating factors. Eberhardt (1997) applied yet another definition of "regulation" as a phenomenon involving two-way actions of the predator-prey system: prey density affects wolf numbers, and wolves affect prey populations. While we endorse the general truth of this concept, we will use terms as defined by Sinclair (1989). After reviewing theoretical concepts of predator-prey dynamics, we will try to apply them to the real world through comparison with field studies of wolves and prey.

Predator-Prey Theory

Two perspectives are necessary to understand wolf-prey interactions: the reproductive potential of the prey, or its annual increment, and the prey-killing potential of the wolf population. The latter is commonly understood as a set of two responses of wolves to their prey: the "numerical response," or change in wolf population size, and the "functional response," or change in individual wolf kill rate. Important features that make each wolf-prey system unique can be examined in the theoretical context of prey reproduction plus wolf numerical and functional responses (Seip 1995), assuming that wolf-caused mortality predominates.

Potential Prey Increment

The annual increment to a prey population is usually expressed in relation to prey density. This is best illustrated by a graphic in which the potential increment (vertical axis) to a population appears as a dome-shaped curve (fig. 5.4) that drops to zero, thus reaching the horizontal axis (corresponding to population density) at the population's carrying capacity (K). At this point, the prey

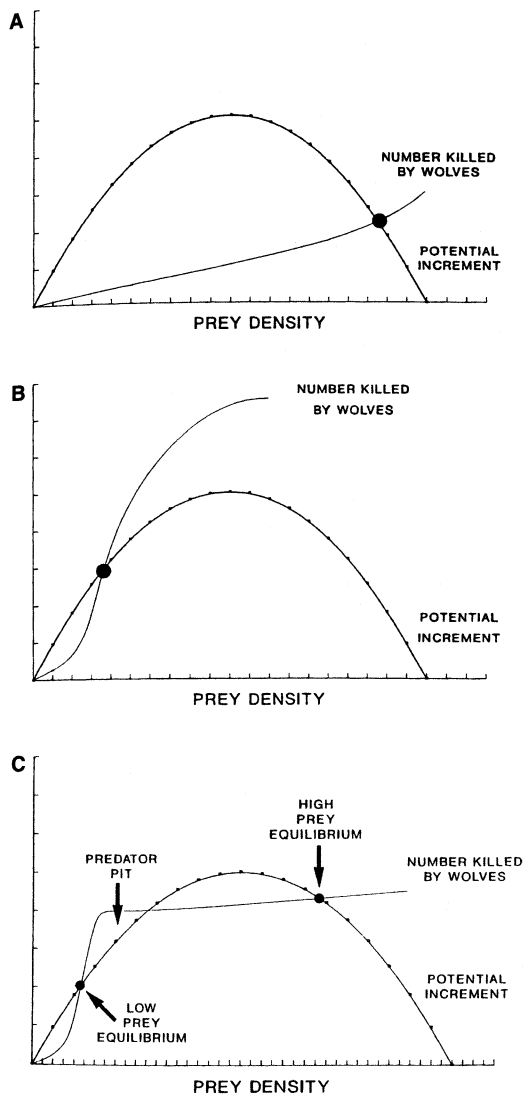


FIGURE 5.4. In theory, prey reproduction can be represented by a hump-shaped "recruitment curve," here labeled "Potential increment." A stable prey equilibrium is possible where this curve intersects the "total response" curve of wolves ("Number killed by wolves"). A variety of prey equilibria are possible, depending on the shape of the total response curve. If wolf predation is density-dependent at low prey densities, prey density may be regulated within a "predator pit." (From Seip 1995.)

population should remain stationary; as prey density approaches this level, the population growth rate is slowed by poor nutrition. (Such curves have been termed yield curves or stock-recruitment curves [Ricker 1954; Caughley 1977].) Potential annual increment is also low when prey density is low, because the population contains few

individuals. The highest annual increment is usually at some intermediate population density at which a herd has grown to substantial size, but not to a size at which nutrition begins to suffer.

At carrying capacity, prey population density is high, and the population is limited by resource scarcity. Evidence of nutritional limitation will be common. This is the state of an ungulate population absent natural predation or hunting mortality. If carrying capacity is overshoot by the prey population, there will be no annual increment, and the population will fall back to carrying capacity. If a prey population at carrying capacity is harvested, whether by humans or wolves, prey numbers will decline and annual increment will be positive. If the additional production is not harvested or taken by other mortality factors, the population will increase back to carrying capacity.

Numerical Response of Wolves

The response of wolf populations to increased prey density will obviously influence their effect on prey. Keith (1983) and Fuller (1989b) found a linear correlation between wolf density and prey abundance; an increase in prey is associated with an increase in wolves (see Fuller et al., chap. 6 in this volume).

Messier's (1994) review of nineteen studies suggested that, where wolves preyed on moose, wolf density increased nonlinearly as moose density rose, and that wolf density plateaued at 58 ± 19 per 1,000 km². However, seven of his nine data points corresponding to high prey density were derived from Isle Royale, and included two periods when wolves were probably limited by disease and its aftermath (Peterson et al. 1998). An eighth point came from Kenai, Alaska, where wolf density was limited by harvest (Peterson, Woolington, and Bailey 1984). Messier did not propose any mechanism that might cause wolf density to stabilize at about 60 per 1,000 km². Isle Royale wolves actually reached a density of 92 per 1,000 km² in 1980 before the likely advent of canine parvovirus retarded wolf numbers; projections of vulnerable prey numbers suggested that wolves could have increased to about 110 per 1,000 km² (cf. Peterson et al. 1998). It has not been demonstrated that any social or territorial restrictions limit wolf density to a level lower than that allowed by food supply (Packard and Mech 1980).

Nevertheless, prey density is not necessarily synonymous with wolf food supply (Packard and Mech 1980).

Especially when prey density is high in a complex, multi-prey system, wolf numbers may not increase in proportion to total prey density. Wolves may rely primarily on one prey species (Dale et al. 1995), at least temporarily, and therefore may not benefit if other prey species increase. For example, wolves in Riding Mountain National Park rely on elk and deer (Carbyn 1983b); they might not respond numerically if moose increased.

On the other hand, moose are a common prey for wolves, providing most of the food for wolves in many areas. Bergerud and Elliott (1998) argued that, if moose (or elk) density were relatively high in such an area, then wolves would increase and sheep and caribou would decline until they equilibrated at fewer than 0.25/km², at which level they would be adequately spaced to avoid wolves. For example, Sumanik (1987) found a high-density Dall sheep (0.68/km²) system in the Yukon, where moose were so scarce (0.06/km²) that wolves supported by moose could not exert much predation pressure on sheep. As a result, sheep were limited by scarce forage and severe winters, not by predation (Hoefs and Cowan 1979; Hoefs and Bayer 1983). Bergerud and Elliott (1998) predicted that if moose were to increase in such a system, wolves would likewise increase, but then Dall sheep would be reduced by wolf predation.

Areas with high prey density often contain multi-prey systems with one or more highly social prey species such as elk or caribou. Wolf encounters with group-living prey are based on the frequency of groups, not of individuals (Huggard 1993b; Weaver 1994). Therefore, increased prey density in such areas would not lead to increased encounters with prey, so wolf response to increased prey density may be lessened for social prey. Bergerud and Elliott (1998) pointed out that the difference between observed wolf numbers and those predicted by prey biomass increased with prey species diversity. They interpreted this finding as evidence of "destabilization" of wolf numbers caused by high prey diversity. However, we believe that the difference more likely results from wolves concentrating their predation on only one or two of the available species.

Despite the rough, large-scale correlation between wolf density and prey abundance, there is much about wolf numerical response that remains unknown. Spatial refuges or migration may make increasing numbers of prey inaccessible to wolves (Krebs et al. 1999), and, depending on patterns of prey selection by wolves, the response of wolf populations to changes in a single prey

species in a multi-prey system may be complex (Dale et al. 1994). Even though most prey biomass for Denali wolves consisted of moose, increased caribou vulnerability arising from several winters with unusually deep snow allowed the wolf population to flourish briefly. The wolf population finally declined as caribou crashed, but the wolf decline was proportionately less because the wolves were supported by other prey (Mech et al. 1998).

The linear relationship between wolf density and prey density is simply a correlation, commonly interpreted as showing the response of wolf numbers to changes in prey numbers. But the general correlation between prey and wolf numbers does not necessarily tell us anything about how a wolf population responds to changes in prey density. This claim is documented by the tortuous pathway actually followed by the wolf and moose population relationship on Isle Royale (fig. 5.5) and the often inverse relationship between wolf and moose numbers there (fig. 5.6). Wolf population change may lag behind that of prey simply because of demographic inertia. At Isle Royale, wolf density closely tracked the abundance of moose at least 9 years old, rather than the total moose population (Peterson et al. 1998), so a decade

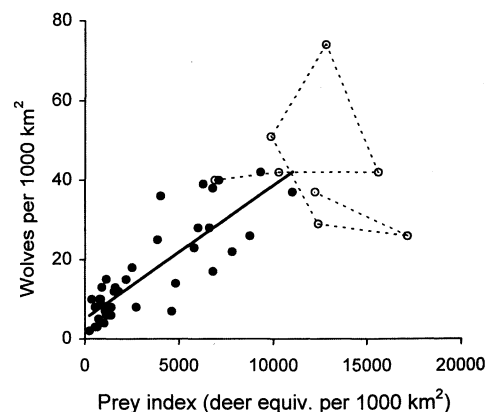


FIGURE 5.5. Linear relationship between wolf density (Y) and prey density (X), based on forty-one studies in North America, shown here as a straight line of the form $Y = 5.12 + 0.0033X$ ($P < .0001$, $r^2 = .71$). Data points (solid circles) were summarized by Fuller (1989b) and Messier (1994). Wolf and moose fluctuations in Isle Royale National Park, shown here as open circles corresponding to 5-year population averages from 1960 to 1999 (Peterson et al. 1998; R. O. Peterson, unpublished data), were excluded from the regression analysis, but are shown here to illustrate the actual path followed by wolf and prey in a single system. The linear regression is commonly used to represent the numerical response of wolves to changing prey density (see also fig. 6.2).

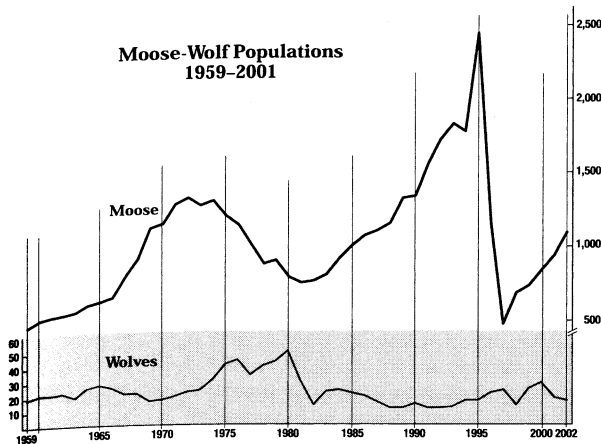


FIGURE 5.6. Fluctuations of wolf and moose populations in Isle Royale National Park from 1959 to 2002 illustrate the generally inverse trends in wolf and moose populations over time. (Data from Peterson et al. 1998; R. O. Peterson, unpublished data.)

may pass between successive changes in moose and wolf populations.

Of course, human persecution and disease may limit wolf numbers quite apart from any influence of prey populations. For example, canine parvovirus emerged in the 1980s as an often lethal disease for wild wolves, at times reducing wolf density in several areas of North America (Mech et al. 1986; Johnson et al. 1994; Wydeven et al. 1995; Mech and Goyal 1995; Peterson et al. 1998).

Wolf Functional Response

Ever since the pioneering work of Holling (1959) on the kill rate of invertebrate prey by deer mice, change in the per capita kill rate of predators with change in prey density (functional response) has been a core feature of predator-prey theory. Holling described three basic types of predator functional responses to increasing prey density: a linear (type I), an asymptotic (type II), and a sigmoidal (type III) increase in the per capita kill rate (fig. 5.7C). While these different types of functional response have important implications for theories about predator-prey stability, the differences may not be of overriding importance in real-world wolf-prey systems (Dale et al. 1994; Van Ballenberghe and Ballard 1994). Conceivably, as prey populations increase and wolves remain constant, the number of prey killed per wolf might tend to increase. Under such circumstances, wolves might simply eat less of each prey animal (Mech et al. 2001), or peripheral members of a pack might be able to

increase their food intake. If prey density continued to increase, however, the individual kill rate would eventually begin to level off as each wolf became satiated.

There are more aspects of functional response than wolf satiation. Broken into its component parts, functional response depends primarily on the search time required to locate a vulnerable prey animal plus the handling time associated with eating it. The time required to actually kill a vulnerable prey animal is usually short. According to theory, as prey density increases, there is a

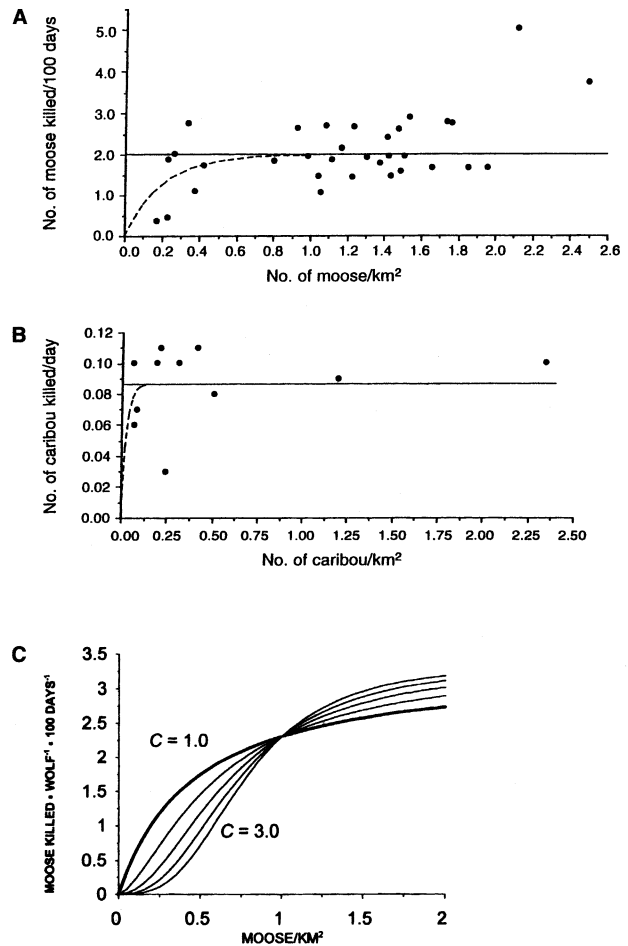


FIGURE 5.7. (A,B) Wolf kill rates for (A) moose (data from Messier 1994) and (B) caribou (data from Dale et al. 1994) were redrawn and interpreted by Eberhardt (1997) as unrelated to prey density except at very low prey levels. (C) Three types of predator functional response, represented by the equation $Y = 3.36X^C / (0.46 + X^C)$, where $C = 1.0$, 1.5, 2.0, 2.5, and 3.0. $C = 1.0$ is a type II functional response (thick line), and $C > 1.0$ is a type III functional response (thin lines). (From Marshall and Boutin 1999.)

progressive reduction in search time (except with prey that herd), allowing the kill rate to increase until handling time alone dictates the kill interval. Handling time comprises feeding time and rest to allow digestion. It, in turn, can be further compressed if prey carcass use is incomplete and feeding time is thus shortened. At the extreme, the kill rate is limited by the time required for an engorged wolf to digest its meal and sleep; thus at this point, wolf functional response must level off. (For actual kill rates, see above.)

Eberhardt (1997), Mech (cited in Ballard and Van Ballenberghe 1998), and Person et al. (cited in Ballard and Van Ballenberghe 1998) argued, and Ballard and Van Ballenberghe (1998) tended to agree, that the functional response concept was inappropriate for application to wolf-prey systems. Because of the inherent difficulties with the concept, there have been relatively few studies of wolf functional response. In a single study area where different wolf packs had access to various numbers of caribou, Dale et al. (1994) found that wolf kill rates were relatively constant across a wide range of caribou densities, although the kill rate tended to decline when caribou density was very low (fig. 5.7B). Eberhardt (1997) found the same with moose, contrary to Messier's (1994) analysis (fig. 5.7A). Although per capita kill rates on Isle Royale increased asymptotically with moose density, only 17% of the variation in kill rate is explained by moose density (Vucetich et al. 2002). In contrast, the ratio of moose to wolves explained 34% of the variation in kill rate. The prospect that moose/wolf ratios better predict kill rates than does prey density has important implications for understanding the strength of top-down influences of wolves on moose (Vucetich et al. 2002).

One of the problems in assessing wolf functional response as a per capita kill rate is that the killing unit for wolves is the pack, not the individual. High kill rates and high pack sizes usually coincide (Hayes et al. 2000). Added members of wolf packs eat portions of prey that would be lost to scavengers if pack size were small, so it seems reasonable to expect pack size to increase faster than kill rate. Finally, the hunting behavior of the pack is probably not dictated by per capita satiation as much as by the satiation of the breeding pair—usually the wolves that take precedence in feeding from kills. Subordinate members of a large pack, with the poorest opportunities to feed, usually remain in their natal pack only if supported by adequate food. Large packs, then, consistently kill more prey, while small packs kill at a disproportionately higher rate (Thurber and Peterson 1993; Schmidt

and Mech 1997). A pack of three wolves on Isle Royale killed, on average, nine moose in 100 days, while a pack 5 times larger killed only 2.8 times as many moose (twenty-five in 100 days) (Thurber and Peterson 1993).

While the functional response concept is a critical part of wolf-prey theoretical models, it has poor predictive power. This is because actual kill rate probably depends more on pack size and on prey vulnerability (which varies with snow depth, population age structure, and nutritional plane) than it does on prey density (see above). Thus we agree with the workers cited above that the concept of functional response, established in laboratory experiments with small mammals and invertebrate prey, is poorly suited to describing wolf predation.

Total Predation Rate

The total number of prey killed by wolves is the product of the number of wolves present and their per capita kill rate. At low prey densities, the total kill is usually small because wolves are scarce. Theoretically, as prey density increases, the number killed by wolves increases disproportionately faster because both wolf numbers and functional responses are increasing, with a multiplicative effect. As a result, the total loss to wolves should be density-dependent, increasing faster than prey density, and thus wolves might be able to regulate prey density (Messier 1994).

According to theory, if prey density continues to increase, wolf numbers or per capita kill rates usually plateau. In reality, we believe there is little reason to expect wolf numbers to plateau if prey density increases (see above). Nevertheless, if the kill rate of wolves does not keep pace with rising prey density, total predation losses may be inversely density-dependent, or "depensatory." The term "depensatory" implies that predation is not density-dependent or regulatory; predators either drive prey to extinction or prey erupt despite predation.

The actual outcome of this contest between predator and prey depends on the extent of predation losses compared with the annual increment of prey. Either one may exceed the other, so prey populations may increase, decline, or, if annual prey increment matches predation losses (plus other mortality), stabilize. Graphically, it is easy to see how prey might stabilize at high or low densities, depending on the height and shape of total predation (total response) and prey increment curves (see fig. 5.4).

Eberhardt (1997) felt it was difficult to assess the effect

of wolf predation on ungulates, owing to the limited quality of the data, the pervasive harvesting of wolves and their prey, and the fact that prevailing wolf-prey theory was based on studies of invertebrates, not wolf-prey systems. Ungulates are often difficult to census, and many assessments of wolf-prey dynamics are based on indices of abundance, or merely informed opinion of likely trends in populations. Furthermore, Eberhardt argued that the use of differential equations in wolf-prey theory is inappropriate, because neither wolves nor their prey reproduce instantaneously, as assumed by these equations. Thus in nonequilibrium systems there will be lags in wolf numerical responses to prey, and, as Holling (1959) pointed out, his "total response" model will be an oversimplification.

Eberhardt (1997) also felt that the equation usually used to describe the functional response of wolves commonly did not fit the actual data on wolf predation. He used a constant kill rate (functional response), a method that Messier and Joly (2000) criticized but Eberhardt (2000) defended (see fig. 5.7). Incorporating this approach into generalized difference equations of the Lotka (1925)-Volterra (1928) genre, he explored whether a wolf-prey model based on wolf-prey ratios instead of prey density might be more suitable.

Eberhardt and Peterson (1999) reexamined wolf abundance and rate of increase in relation to prey biomass and the conclusion of Eberhardt that wolf and prey numbers usually were proportional, with an average of over 200 deer-equivalents per wolf (Eberhardt 1998). Eberhardt and Peterson (1999) revised this figure to 122 deer-equivalents per wolf (equivalent to 40 elk or 20 moose per wolf, based on Keith's [1983] estimates of relative biomass). When this figure is combined with an average wolf kill rate (estimated at 6.9 moose/wolf/year) and a productivity of 7.8 moose/wolf/year (assuming an even sex ratio, 13% yearlings, and a 90% pregnancy rate and single calves for moose over 2 years old; see Peterson [1977] and Schwartz [1998]), it is apparent that wolves can harvest moose at a rate close to their maximum annual increment (Mech 1966b, 163). Thus wolves could potentially regulate prey abundance (Eberhardt 1997), and the combined effects of predation by both wolves and humans may lead to prey declines (Eberhardt et al. 2002).

Multiple Equilibria: A Theoretical Possibility

Much has been made of the concept of "equilibria" in wolf-prey systems, sometimes in the context of wolf con-

trol programs (Haber 1977; Walters et al. 1981; Messier and Crête 1985; Seip 1995). A graphic model illustrates that if the total predation curve intersects the annual increment curve in a certain way relative to prey density, then three potential equilibria between wolves and prey might result (see fig. 5.4). One of the equilibria would be unstable, and prey would not remain at this level, while the other two would be stable.

Theoretically, if a wolf-prey system existed at a low equilibrium (called a "natural enemy ravine" [Southwood and Comins 1976] or a "predator pit" [Walters 1986]) and if the total predation curve were lowered temporarily (as when wolf numbers are reduced by control programs), prey could escape predation and increase to a high equilibrium. Alternatively, prey could reach a high equilibrium if prey productivity improved dramatically. Having achieved a high equilibrium, prey would, in theory, remain there even if wolves were allowed to recover. This conclusion would be attractive to wildlife managers, suggesting that a long-term increase in prey might result from short-term predator control. But does it really work this way?

A theoretical condition for the existence of multiple equilibria or "two-state systems" is that total losses to predation be density-dependent at low prey densities (Messier 1995b). In addition, if a wolf reduction allows prey to escape from a low to a high equilibrium, then prey should remain at the high-density equilibrium even after predator numbers are restored (Skogland 1991). Finally, dramatic prey population "outbreaks" should occur when there is an increase in herd productivity, as might occur following substantial habitat improvement (Van Ballenberghe and Ballard 1994; Kunkel and Pletscher 1999). During the 1980s and 1990s there were extensive efforts, primarily through wolf control in Alaska and the Yukon, to induce prey populations to increase to a high stable equilibrium, but none was successful, except possibly that in interior Alaska between 1976 and 1982 (Boertje et al. 1996) (see below).

The degree to which wolf predation is density-dependent at low prey densities should affect the persistence and stability of prey populations. A type II functional response, with increasing slope as prey density decreases, would allow less prey persistence and stability than a sigmoid type III curve because predation would be more apt to drive prey to extinction. Efforts to distinguish between type II and III curves underlie recent efforts to assess wolf predation effects (Messier 1994; Dale et al. 1994).

Marshal and Boutin (1999), however, point out that the statistical power to distinguish among these curve types is very low because of the low sample sizes and high variability typical of field studies. They suggest bypassing this analysis and directly measuring mortality rates for moose at low and intermediate densities. They proposed two possible ways to tell whether wolf predation is density-dependent, and thus regulatory, at low prey densities (Walsh and Boutin 1999): first, if moose density can be induced to increase by removing wolves, then the proportion of moose killed by wolves should increase from before wolf removal to after wolf recovery; second, if moose density is reduced, the proportion of moose killed by wolves should decrease. Regardless of whether wolf predation regulates prey, wolf predation can still be considered a limiting influence on prey density.

Most studies of wolves and prey have involved relatively simple systems with one to two prey species. As the prospect and reality of wolves in the northern Rocky Mountains emerged in the 1980s, interest grew in the nature of wolf-prey dynamics in systems with as many as five prey species. Building on the pioneering work of Cowan (1947) and Carbyn (1974), recent studies by Huggard (1993a,b) and Weaver (1994) in Jasper and Banff National Parks have sought to understand the apparent preference of wolves for certain prey species.

Huggard (1993b) assessed prey abundance and predation patterns for two packs in the Bow River Valley of Banff National Park. Occupying lowland habitats were elk, mule deer, and moose, while bighorn sheep and mountain goats inhabited primarily steep slopes and higher elevations. The sheep and goats overlapped little with the wolves and were infrequently killed. Elk biomass exceeded deer biomass by an order of magnitude, and moose were uncommon. As in the earlier studies, elk predominated among wolf kills, and based on the number of encounters with prey, there was no apparent preference for any prey species.

Nevertheless, Huggard (1993b) revealed greater complexities in this system. Wolves encountered many elk in groups in predictable locations, while they encountered deer more randomly. For elk, the herd was the basis for wolf encounters; with many animals in a herd, the chance of a successful kill was higher than for an individual prey encounter. Hunting wolves appeared to key in on predictable elk herds, with a high probability of making a kill, and they also killed elk and deer during random encounters while traveling between predictable

elk herds. Huggard (1993b) argued that prey encounter rate was the most important determinant of wolf diet, because as prey density changes, the unique grouping tendencies and habitat selection patterns of each prey species result in different responses by wolves. Based on a simple model of functional response, Huggard showed that the changing pattern of encounter rates, by itself, would generate different patterns of selectivity by hunting wolves as prey density changed. For example, with constant deer density but declining elk density, selection for elk would increase as wolves concentrated on predictable elk herds.

In the real world, additional factors contribute to more complexity: wolves may have inherent preferences for certain prey based on experience (see above), and capture success may vary as prey density and vulnerability change. Snow conditions affect each prey species in a unique manner, and even the carcass use patterns of wolves (which vary with pack size and the presence of scavengers) affect their response to changing prey density (Mech et al. 2001).

From the foregoing discussion, it is apparent that the numerical and functional responses of wolves are grossly oversimplified when modeled simply against prey density, and our limited understanding usually prevents realistic elaboration of the existing models. Consequently, trying to predict wolf responses in a multi-prey system is quite a primitive business.

Wolf Predation in the Real World

It has been repeatedly stressed that critical features of wolf-prey dynamics will differ between wolf populations that are naturally regulated and those that are harvested by humans; additionally, simple systems with a single predator and prey will be fundamentally different from those with either alternative prey or additional predators (such as bears) (Filonov 1980; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994). For any given wolf-prey system, there will always be unique characteristics that must be understood before the effect of wolf predation can be predicted. For example, factors that limit wolf populations, including control programs, may greatly influence wolf-prey dynamics (Seip 1995).

Wolf control by wildlife managers has always been controversial. In 1994, Governor Tony Knowles of Alaska suspended that state's wolf control program and asked the National Academy of Sciences to undertake a scien-

tific review and economic analysis of wolf and bear management in Alaska. The resulting committee report (National Research Council 1997) reviewed eleven case histories of wolf control in Alaska, the Yukon, and British Columbia. The committee concluded that wolves and bears in combination could limit prey at low numbers for many years, and that predator reduction might hasten the recovery of prey. An increase in prey density was demonstrated in only three of the eleven cases, but increased juvenile survival after predator reduction was a common finding.

The three cases of increased prey density (National Research Council 1997) involved Game Management Unit (GMU) 20A in east-central Alaska; Finlayson, Yukon Territory; and northern British Columbia. They illustrated the committee's conclusion that wolf control is unlikely to result in increased prey populations unless a very high proportion of resident wolves are killed annually over a large area for at least 4 years. Such a high level of wolf control is necessary to prevent local reproduction and rapid recolonization from surrounding areas from bringing the wolf population rapidly back to its previous levels (Boertje et al. 1996; Bergerud and Elliott 1998; Hayes and Harestad 2000a).

In GMU 20A, wolves were killed from aircraft for 7 years, after a combination of overharvest and severe winters had reduced moose to a low level ($0.2/\text{km}^2$). Over $17,000 \text{ km}^2$ ($6,640 \text{ mi}^2$), 337 wolves were killed during 1976–1982, reducing wolf density to about 44% of its pre-control level for 6 years (fig. 5.8; Boertje et al. 1996). During the 7 years after official control ceased, another 190 wolves were killed by private hunters, but wolf density nevertheless increased to 80% of the pre-control level. During the 7 years of wolf control, moose density increased from 0.2 to $0.5 \text{ moose}/\text{km}^2$, and in the next 15 years to $1.3 \text{ moose}/\text{km}^2$. This increase was high enough to cause concern that a severe winter might cause a moose die-off (Boertje et al. 1996).

In fact, beginning in 1989–1990, 4 years in 5 brought deep snow (90 cm or 36 in), but the moose population continued to increase. Caribou, on the other hand, declined with the severe winters, after increasing from 0.2 to $0.9 \text{ caribou}/\text{km}^2$ in the 14 years during and after wolf control, when winter weather was favorable. While wolf control apparently led to impressive increases in caribou and moose herds, it must also be realized that hunting of both prey species was also greatly curtailed (National Research Council 1997), and it remains un-

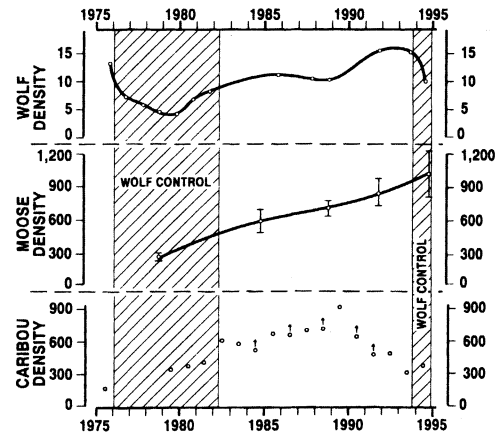


FIGURE 5.8. Population densities for wolves, moose, and caribou in Game Management Unit 20A in interior Alaska, 1975–1994. Moose estimates include 90% confidence intervals. Caribou and moose density increased during and after 7 years of wolf reduction when winter weather was benign. Caribou declined, but moose continued to increase during four consecutive severe winters from 1989–1990 to 1992–1993. (From Boertje et al. 1996.)

known what would have transpired if winter weather had not cooperated.

A 6-year wolf reduction experiment conducted in Finlayson, Yukon Territory, was also followed by increases in moose and caribou (National Research Council 1997). However, an upper prey equilibrium was not maintained; when wolf control ended, prey populations began to decline. Between 1983 and 1989, over $23,000 \text{ km}^2$ ($9,000 \text{ mi}^2$), 454 wolves were removed, mostly shot from helicopters, producing an 85% reduction in wolf density. As in central Alaska, harvest of prey by human hunters was also greatly restricted.

Caribou density rose from about $0.1/\text{km}^2$ in 1983 to $0.3/\text{km}^2$ in 1990 as the proportion of calves almost doubled (from 26 to 50 calves/100 cows). Moose density was not estimated before wolf control began, but in 1987, after 4 years of wolf control, there were 67 calves/100 cows, and, based on hunting statistics, moose density was increasing. In 1996, 6 years after wolf control ended, the proportion of moose calves had dropped to about 30/100 cows. Likewise, in the 4 years after wolf control ended, there were about 32 caribou calves/100 cows, and caribou density declined to $0.2/\text{km}^2$. This study revealed wolf predation as a major limiting factor for these prey species, but it raised little hope for an upper equilibrium for prey in the absence of continued wolf control.

Similar results were reported from northern British

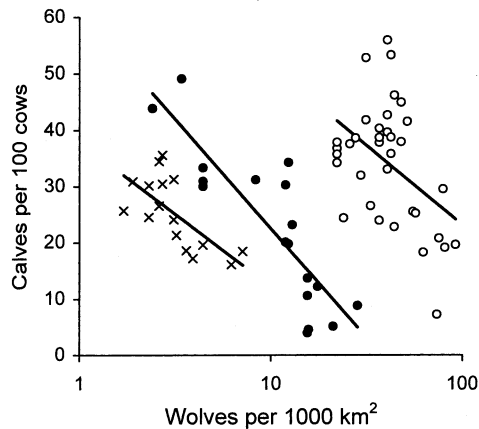


FIGURE 5.9. The relationship between moose calf abundance and wolf density is consistently negative, yet differs geographically (Xs, data for Alaska from Ballard et al. 1987; solid circles, data for British Columbia from Bergerud and Elliott 1998; open circles, data for Isle Royale from R. O. Peterson, unpublished data). Wolf control caused variation in wolf density in the Alaska and British Columbia study areas, but on Isle Royale wolf density was correlated with the number of old moose (Peterson et al. 1998). Wolf density varied between study areas probably because of differences in prey density. Note that moose populations usually increase when calf abundance exceeds 24–26 calves per 100 cows (Peterson 1977; Bergerud and Elliott 1998). Linear regression lines all had negative slopes ($P < .01$) and $r^2 = .47$, $.73$, and $.20$ for data shown for Alaska, British Columbia, and Isle Royale, respectively.

Columbia (Bergerud and Elliot 1998). In several study areas, wolves were reduced by 60–86% for 3–4 years. The proportion of juvenile prey (at least 5 months old) increased twofold to fivefold, and population densities increased for all four large ungulates in the area: moose, caribou, elk, and Stone's sheep. Interestingly, this study suggested that, for all four prey species, an average recruitment of 24 juveniles/100 females was sufficient to balance average mortality (fig. 5.9). Where wolves were not reduced, average recruitment for moose and sheep was 14–23 young/100 females, while in areas of wolf control there were 32–45 young/100 females. Projections suggested that, without wolves, average recruitment for all four prey would be 53–57 young/100 females. As in the Yukon experiment, the British Columbia data did not suggest that an upper equilibrium could be maintained without continued wolf reduction.

Seven of the eleven case studies (National Research Council 1997) involved reduction of only wolves, not bears, yet bears prey heavily on newborn ungulates. In the Nelchina Basin, a 61,600 km² (24,000 mi²) area in

south-central Alaska, 60 wolves were killed in an experimental area of 7,262 km² (2,837 mi²) during 1976–1978. Public wolf harvest outside the experimental area also increased, reducing wolf density throughout the Nelchina. Ballard et al. (1987) concluded that for this and other reasons it was not possible to fully evaluate the effect of wolf predation on the moose population. Nevertheless, autumn moose calf/cow ratios were negatively related to wolf density (see fig. 5.9).

A companion study of moose calf mortality conducted in 1977–1978 involved determining the cause of death for 120 moose radio-collared soon after birth (Ballard et al. 1979, 1981). In the first 6 weeks of life, 55% of the moose calves died. Predation accounted for 86% of natural deaths, and brown bears accounted for 91% of those deaths. Wolves, reduced to a low density (2.7/1,000 km²), were responsible for only 4–9% of the predation deaths, and estimated recruitment greatly exceeded the proportion removed by wolves. After brown bear density was reduced 60% by moving bears away, calf survival increased. Most of the bears returned, however, and calf survival returned to pre-bear-removal levels.

Van Ballenberghe and Ballard (1994) listed another four areas where predation was judged to be a major limiting factor during specific periods. However, because bears coexist with wolves throughout wolf range, the difficulty of evaluating the effects of wolf predation alone has bedeviled scientists and game managers alike.

The wolves secluded in Isle Royale National Park, probably the world's safest wolf sanctuary, provided one of the most impressive natural wolf control experiments by their population crash during 1980–1982, which was circumstantially linked to canine parvovirus (Peterson et al. 1998). In 1981, coincident with the wolf crash, the proportion of moose calves shot from an average of about 22/100 cows to, briefly, 60/100 cows (Peterson and Page 1988). Over the next 15 years, with wolves unexpectedly few, moose increased to over 4/km², about ten times higher than usual moose densities in mainland areas of North America (Messier 1994). Thus the limiting nature of wolf predation was revealed (Peterson 1999).

The high level of moose on Isle Royale led to reduced growth of balsam fir (McLaren and Peterson 1994), which moose eat in winter, demonstrating that the indirect effects of wolf predation in an ecosystem can be significant. This cascading relationship from wolf to moose to fir recalls Aldo Leopold's (1949) essay, "Think-

ing like a mountain,” in which he proposed that the integrity of mountains themselves was influenced by wolves in this manner. Of course, at the top of this cascade was the lowly canine parvovirus.

Wolf predation appears to fit the generalization (Hairston and Hairston 1993, 379) that “predation is a major source of herbivore mortality in terrestrial communities, and grazing on plants is held at a lower level than would otherwise be the case.” Similarly, Krebs et al. (1999, 447) concluded that “all vertebrate herbivores are limited primarily in abundance by predation unless they have evolved an escape mechanism in space or time.”

Limiting Effect of Wolves on Prey

There has been much attention to theoretical models in attempting to explain the effects of wolves on prey populations (Mech and Karns 1977; Walters et al. 1981; Van Ballenberghe 1987; Crête 1987; Skogland 1991; Boutin 1992; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994). The primary scientific debate centers on whether wolf predation regulates prey at low-density equilibria, with predation rate increasing faster than prey density, or whether it acts more simply as a limiting factor that, when combined with bear predation and other limiting factors, leads to prey densities far below the carrying capacity set by food supply. As in the above case studies, while prey have been induced to increase via predator control, they tend to decline again after predators recover (Gasaway et al. 1992). This outcome supports the notion that wolf predation limits, but does not regulate, prey populations.

The moose population on Isle Royale is highly dynamic, and wolves may well contribute to this instability (Peterson, Page, and Dodge 1984). Statistical analysis suggests that the observed moose dynamics arise from dynamics that alternate between periods of wolf increase and decrease (Post et al. 2002). Specifically, during years of wolf decline, moose exhibit strong direct density dependence, and during years of wolf increase, moose exhibit only weak direct density dependence and strong delayed density dependence. These patterns suggest that moose are strongly attracted to an equilibrium during wolf decreases and exhibit unstable dynamics, characteristic of a cyclic population, during wolf increases.

At low prey densities, the distinction between regulation and limitation hinges on whether wolf predation is density-dependent. Two studies have claimed that wolf

predation is density-dependent at low prey densities. Messier and Crête (1985) estimated losses to wolf predation at three low moose densities in Quebec and argued that they had evidence of density dependence. However, others found the evidence equivocal (Van Ballenberghe 1987; Boutin 1992). Pooling data from several studies in North America, Boutin (1992) showed that wolf predation rates were density-independent and were remarkably constant over a wide range of moose densities.

Bergerud (1992) also argued that wolf predation is density-dependent, based on his analysis of correlations between calf survival, wolf density, and prey density for caribou and moose. Bergerud's hypothesis is that a major strategy to reduce predation is “spacing out” (see above), and he relies heavily on the logic that predation at low prey densities *must* be density-dependent; it seems reasonable that predators should be able to kill a higher proportion of young animals if they are clumped instead of spaced out (e.g., Miller's [1983] surplus killing of caribou calves by wolves). While Bergerud's analysis provides evidence that predation by both wolves and bears can be strongly limiting, his claim that wolf predation is generally regulatory is based more on reasoning than on actual evidence.

Most reviewers have stressed that the rather scarce empirical data used to evaluate alternative hypotheses have serious limitations. Regardless of whether wolf predation is density-dependent or not, bear predation seems to be additive and density-independent (Boertje et al. 1988; Van Ballenberghe and Ballard 1994), and wolves coexist with bears throughout their North American range, except on Isle Royale, and in many areas of the Old World (Filonov 1980). Even if wolf predation is density-dependent, it is usually overlain by bear predation, which apparently is not (Gasaway et al. 1992; Van Ballenberghe and Ballard 1994).

Limited by predation, prey populations will rise and fall at irregular intervals based on demographic and environmental factors that influence losses to predators (Van Ballenberghe 1987). These factors include relative numbers of predator and prey (Mech 1970, 277; Eberhardt 1997); snow depth, which influences wolf kill rate (Mech and Frenzel 1971a; Mech and Karns 1977; Peterson 1977; Nelson and Mech 1986c; Mech, McRoberts et al. 1987; Mech et al. 1998; DelGiudice 1998; Post et al. 1999; Jedrzejewski et al. 2002; Hebblewhite et al. 2002; Kunkel et al., in press); and fluctuations in other predator and prey species in the system (Kunkel et al. 1999; Kunkel

and Pletscher 1999). Thus a severe winter, a string of mild winters, or habitat rejuvenation by fire may induce prey populations to fluctuate by altering prey reproductive output or losses of prey to predators.

While many factors may influence prey density, the basic conclusion is that wolves and bears always help limit prey numbers, as demonstrated by the study in GMU 20 (fig. 5.10). An extreme example is seen in the 3,000 km² (1,170 mi²) area of poor habitat in northeastern Minnesota where, during a series of severe winters, wolves decimated a white-tailed deer population (Mech and Karns 1977), and deer did not repopulate the area for at least the next 30 years (L. D. Mech and M. E. Nelson, unpublished data).

Gasaway et al. (1992) argued that, for moose, each additional predator species resulted in a stepwise reduction in density. If we consider wolves, brown bears, black bears, and humans as the potential predator guild for moose and caribou, it is clear that prey density depends on the number of predator species (fig. 5.11). Prey density can be quite high if the wolf is the only carnivore present, as in Isle Royale National Park. However, throughout their global range, wolves everywhere else coexist with human hunters or bears.

Although wolves do help limit or retard the growth of their prey populations, it is also clear that these predators do not necessarily hold prey numbers down. Mech (1970, 268) distinguished between systems where wolves controlled their prey (and where removing wolves would allow the prey population to increase) and where they did not, and concluded that they did not where prey/wolf ratios were greater than 25,000 pounds (11,364 kg) of

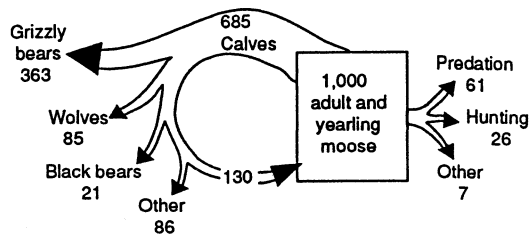


FIGURE 5.10. From a hypothetical pre-calving population of 1,000 moose in east-central Alaska (Game Management Unit 20E), an average of 685 calves are born, and about 19% of those calves survive to the age of 1 year. Most mortality is caused by predators, especially brown bears. For moose older than 1 year, average mortality was 9.4%, and predation by bears and wolves was the largest source of mortality. Mortality from hunting was less than 3% annually. (From Gasaway et al. 1992.)

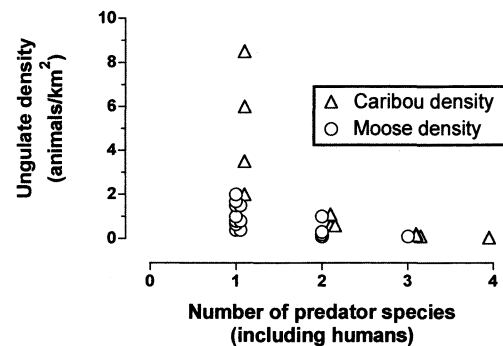


FIGURE 5.11. Ungulate density in relation to the number of predator species present, including black bears, brown bears, wolves, and humans (from Peterson 2001).

prey/wolf. More recent cases in which prey populations increased despite the presence of wolves include the moose on Isle Royale (Peterson et al. 1998), caribou in Denali National Park (Adams and Dale 1998a; Mech et al. 1998), and deer in northeastern Minnesota (Mech 1986; Nelson and Mech 1986a, 2000; Mech, McRoberts et al. 1987). In the first two cases, the prey/wolf ratio exceeded the above level, but in the last case it did not. In all three cases, the prey population trends were related to snow depths, which affect prey nutrition and thus the degree to which prey are vulnerable to predation (see also Jedrzejewski et al. 2002).

Additive versus Compensatory Mortality

In trying to assess whether wolves are controlling a prey population in any given situation, it would be helpful to know the extent to which wolf predation is compensatory (Errington 1967) to other mortality factors and the extent to which it is additive (Mech 1970, 268). When wolf predation is compensatory, it is only substituting for other mortality factors. For example, if wolves took only deer that would have starved to death otherwise, then wolf predation would be compensatory.

Usually the situation is more complex, however, with wolves killing some of the prey individuals that would have died from other causes and some that would not have. As indicated above, bear predation usually seems to be additive to wolf predation, although when wolves are removed from a system, bear predation may compensate for wolf predation on calves (Ballard et al. 1987). In certain Russian nature preserves, prey mortality shifted among various predators in a compensatory way

as various carnivores were controlled by humans (Filonov 1980).

As discussed earlier, it is with young-of-the-year that the least is known about the degree to which wolf predation takes inferior animals and thus the extent to which it is compensatory. How many of the calves that wolves kill would have lived otherwise? The answer to this question would help us considerably in determining the effect of wolves on prey populations, so this is an area that needs considerably more research.

Disagreement about Wolf Effects on Prey Numbers

Why is there still no scientific consensus on the significance of wolf predation in prey population dynamics? One reason is that scientists have studied a wide range of wolf-prey systems, each with a combination of ecological factors that renders it unique (Mech 1970, 268). Factors of importance include different combinations of prey species (wolves supported by one prey species may have a disproportionate influence on alternative prey, as with caribou affected by wolves that subsist primarily on moose [Bergerud 1974; Seip 1995]); other predator species (mountain lion [Kunkel et al. 1999], grizzly bear, black bear); a wide range of human effects on both predators and prey (confounding any understanding of predator-prey interaction); differences in the inherent productivity of habitats and of prey populations (Seip 1995; National Research Council 1997); and regional differences in the importance of winter snow conditions (Coady 1974; Mech and Karns 1977; Mech et al. 2001; Hebblewhite et al. 2002). Any of the above factors may influence the degree to which prey are limited by wolf predation, both in different geographic regions and at different times in the same area (Mech, McRoberts et al. 1987; Mech et al. 1998; DelGiudice 1998).

A second reason that disagreement persists is that wolf-prey systems are inherently complex, with population dynamics affected by nonlinear predator-prey linkages, multi-trophic-level interactions (Bergerud 1992; McLaren and Peterson 1994; Hayes and Harestad 2000b; cf. Krebs et al. 1995 for another predator-prey system), and even predator and prey mental states (Brown et al.

1999). Finally, data on wolf and prey population densities often are inherently neither precise nor accurate, and measured predation rates by wolves also show great variation (Schmidt and Mech 1997; Marshal and Boutin 1999), leaving much room for differing interpretations of field data.

In summary, although considerable debate still rages over several theoretical issues related to wolf-prey interactions, we find general agreement on a few key points. First, wolf predation can be an influential limiting factor for prey populations, especially where wolves themselves are not limited by harvest. Second, when wolves coexist with grizzly bears, black bears, or both, the combined effects of these predators are usually sufficient to reduce primary prey populations to levels below that which could be supported by their forage base. (That is not to deny that food and other environmental factors may also influence prey dynamics.) Third, wolves have their greatest demographic effects on prey via predation on young-of-the-year (Pimlott 1967; Mech 1970).

In this chapter, we have tried to discuss the very essence of the wolf: how the animal interacts with its prey in order to eat, survive, and reproduce. The coevolution of the wolf and its prey, an ongoing contest during which the prey must survive in the face of constant threat by the wolf, and the wolf must succeed in overcoming specialized prey defenses often enough to survive, is scientifically one of the most intriguing aspects of wolf biology. Likewise, it is most captivating—and disconcerting—to members of the lay public who are interested in the wolf, negatively or positively.

The innate need of the wolf to attack large prey is what most often brings the creature into conflict with humans (see Fritts et al., chap. 12, and Boitani, chap. 13 in this volume). In addition, the wolf's wide geographic distribution and diverse prey base result in great variation in interactions between the wolf and its prey. Thus, perhaps it is understandable that, even after much study, scientists still disagree on the precise nature of several aspects of this fascinating topic.

Ecosystem Effects of Wolves

L. David Mech and Luigi Boitani

Wolves form a major force in the ecosystems of which they are a part. On a circumpolar basis, these animals represent probably the single most important predator on large mammals (but cf. Murphy et al. 1999).

Like any other species, wolves inevitably influence other ecosystem components and processes, but they may do so in a more obvious way because their effects on other vertebrate species are more prominent and more easily observed. Several primary effects of wolves have long been recognized (Mech 1970): (1) the sanitation effect (culling of inferior prey individuals), (2) control or limitation of prey numbers, (3) stimulation of prey productivity, (4) an increase in food for scavengers, and (5) predation on non-prey species.

We have covered some of these primary effects in detail in various chapters of this volume. However, these primary effects cascade or "ripple" (N. A. Bishop, personal communication) through the ecosystem, causing other important changes. Unfortunately, the further down the ecological cascade from the wolf itself, the less we know about its effects, and the less certain we are about what we know. Thus, for now, all we can do is highlight a few of the secondary or tertiary effects of the wolf, which we will label "indirect" effects to distinguish them from its primary, or "direct" effects.

There is a tendency to view the ecological effects of wolves as "good" or positive, probably because one of the main postulates of conservation biology views ecological complexity as good and simplification of ecosystems by humans as bad. From this perspective, many of the primary effects mentioned above can be considered positive. However, in the interest of science and objectivity, we advise against this outlook, for two reasons. First, science does not really know enough about many of the cascading effects to judge the extent of their positive or negative effects on other elements of ecosystems—and many of them may well be both. Second, claims about positive or negative, good or bad, are human value judgments and differ depending on which humans make them. The fact that wolves tend to spread the hydatid tapeworm,

which occasionally is detrimental to humans (see Kreeger, chap. 7 in this volume) is an example.

The reintroduction of wolves into Yellowstone National Park is a useful case study to show the complexity of the role of wolves in ecosystems. Two main types of cascading effects have gained scientific attention: (1) those resulting from the wolf's interference competition with coyotes, and (2) those resulting from predation on ungulate herds. Although there has been little time yet for studies of these phenomena in Yellowstone, there has been considerable speculation about them.

Effects of Coyote Reduction

Wolves have reduced coyote numbers in part of Yellowstone (see Ballard et al., chap. 10 in this volume), and predictions are that this reduction will result in an increase in red foxes, which without wolves are more subject to interference competition from coyotes (Crabtree and Sheldon 1999a,b; Singer and Mack 1999). Reductions in coyotes could also lead to increases in their prey, which in turn could lead to increases in several other mesocarnivores (Buskirk 1999).

On the other hand, an increase in the year-round carrion supply in the form of numerous wolf-killed ungulates might support an increased mesocarnivore population quite aside from the direct killing of coyotes by wolves. That increase, in turn, might dampen small mammal numbers, which could have a differential effect on various of the mesocarnivores. Such effects would not necessarily be constant, but most probably would vary over time and space depending on other ecological conditions, including weather. Whether an increase in mesocarnivores is positive or negative depends on one's viewpoint. Mesocarnivores are considered "important ecologically" for various reasons (Buskirk 1999, 166), but may also contribute to the "loss of ground-nesting birds and probably other small vertebrates" (Terborgh et al. 1999).

Although the indirect effects of wolves on mesocarnivores and their prey are complex and dynamic, the influence of wolves on more diverse taxa, such as birds (Stahler 2000) and insects (Sikes 1994), is much more so. Most effects on these taxa are probably related to their interactions with carrion from wolf kills

and with mesocarnivores and their prey. Certainly with wolves in the system, there will be changes in the numbers and distributions of these creatures and, in turn, of those they interact with. But accurately predicting the direction of those effects and any net benefit or detriment may forever be impossible.

Wolf Effects on Prey

Indirect effects of wolves on prey could be caused by structural changes in prey herds, such as changes in the species, age, sex, and condition of the standing crop; by changes in prey distributions, behavior, and movements; and by changes in prey numbers.

Because wolves tend to kill primarily the oldest, youngest, and most debilitated and undernourished members of prey herds, such herds under the influence of wolves tend to be made up of individuals of prime age, condition, and health, and therefore of highest productivity (Mech 1966b; Bubenik 1972; Schwartz et al. 1992). Over tens of thousands of years of such natural selection, the antipredator defenses and adaptations of prey should tend to become keener as wolf and prey continue their arms race. Antipredator behavior affects the movements and distributions of prey. Thus, for example, in Yellowstone National Park, some predict that elk may increase their use of forest cover, bison may seek tree cover during snow-free periods, and bighorn sheep may abandon the gentler slopes (Singer and Mack 1999).

Probably the most pervasive and yet diffuse indirect effects of wolf predation come from reductions in prey numbers. Whether or when wolves control, limit, or regulate their prey, and under what conditions, is discussed in this chapter. There certainly are documented cases in which wolves have led to fewer prey. Numbers of prey can influence vegetation and cause ripples further down and out from the trophic cascade; that much is obvious. The question is, just what are these effects, how do they work, and what are their consequences?

Controversy and confusion have arisen over whether such effects tend to flow from the bottom trophic level (vegetation) upward or from the top level (wolves) downward (Schmitz et al. 2000). Long-term studies of the wolves, moose, and vegetation on

Isle Royale (Mech 1966b; Jordan et al. 1967; Peterson 1977) have served as the catalyst for debate on this issue. Two views of the workings of the Isle Royale ecosystem have emerged.

Isle Royale wolf numbers tend to follow the trend in moose numbers with a lag of 7–10 years (Peterson, Page, and Dodge 1984). Since herbivore numbers depend on vegetation quality and quantity, and the latter is modified by snow conditions (Mech, McRoberts et al. 1987; McRoberts et al. 1995; cf. Messier 1991), this finding suggests a bottom-up flow of effects. On the other hand, it also appears that high moose numbers tend to follow low wolf numbers, and that moose browsing on balsam fir, and thus fir growth, is related to moose numbers (McLaren and Peterson 1994). This finding suggests top-down flow (but cf. Schmitz et al. 2000).

In other wolf-prey systems, evidence has accumulated that snow depth, modulating vegetation availability, drives the systems, a bottom-up flow. Furthermore, there is no reason to believe that forces in all food chains act in the same direction. The Isle Royale top-down flow was postulated only for the wolf-moose-balsam fir chain, but fir is eaten during only part of the year, and even during that time, it constitutes only 59% of the moose diet (McLaren and Peterson 1994). Food chains involving other plants could evince a bottom-up influence; Boyce and Anderson (1999) postulated that such would be the case in Yellowstone. Discussion on the prevalent direction of flow of effects will never end and may well be a trivial issue, as it focuses on only a few interactions of selected trophic chains within an ecosystem. Recent findings of a long-term study of northern ecosystems in the Yukon show the largely unpredictable interaction between simple species relationships and complex stochastic events that affects ecological processes at a variety of spatial and temporal scales (Krebs et al. 2001).

Regardless of the direction of forces in wolf-prey ecosystems, wolves must exert some indirect influence on the vegetation through predation on the main herbivores in a system. Some historical evidence has been offered that successful aspen recruitment ceased after wolves were removed from the Yellowstone ecosystem in the 1920s (Ripple and Larsen 2000) and

that aspen growth increased after wolf restoration (Ripple et al. 2001).

On a broader scale, Cr  te et al. (2001) have shown what they consider to be negative effects of herbivores on 197 plant taxa eaten by white-tailed deer, moose, and caribou/reindeer and positive effects on only 24. Presumably, then, wolf predation on these ungulates would bring reverse effects on the plants by reducing the ungulates. However, assigning positive and negative values to these effects is, as mentioned earlier, controversial. For example, claims have been made by some (Wagner 1994) that biodiversity—generally considered positive ecologically—is reduced by ungulate feeding, while others claim the opposite (Boyce 1998).

Wolves do affect ecosystems through multiple interacting ecological processes whose nonlinear effects confuse the superficial observer. It is possible that much of the discussion on the role of wolves within ecosystems is due to the mismatch of data collected under different sampling scales. We do not claim to know whether the wolf's effects are positive or negative, what its net effect is, or whether its effects are of any great consequence ecologically. We thus favor continued research into these issues to help solve the unknowns about this interesting and complex subject.