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6

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A LARGE, DARK WOLF poked his nose out of the pines in Yellowstone National Park as he thrust a broad foot deep into the snow and plowed ahead. Soon a second animal appeared, then another, and a fourth. A few minutes later, a pack of thirteen lanky wolves had filed out of the pines and onto the open hillside.

Wolf packs are the main social units of a wolf population. As numbers of wolves in packs change, so too, then, does the wolf population (Rausch 1967). Trying to understand the factors and mechanisms that affect these changes is what the field of wolf population dynamics is all about. In this chapter, we will explore this topic using two main approaches: (1) meta-analysis using data from studies from many areas and periods, and (2) case histories of key long-term studies. The combination presents a good picture—a picture, however, that is still incomplete. We also caution that the data sets summarized in the analyses represent snapshots of wolf population dynamics under widely varying conditions and population trends, and that the figures used are usually composites or averages. Nevertheless, they should allow generalizations that provide important insight into wolf population dynamics.

What Is a Wolf Population?

Trying to define a wolf population is problematic. As chapter reviewer Bruce Dale (personal communication) reminded us, two adjacent wolf packs may each depend on separate prey bases and thus respond independently to prey changes. In that respect, they could be regarded as separate populations. However, in regard to a disease outbreak that might affect many adjacent packs, the entire group affected could be considered a population. Or, genetically, all the wolves in the contiguous range from northern Alaska through Canada into Minnesota, Wisconsin, and Michigan could be thought of as one population.

There is no convention applicable here: a wolf population can be whatever interacting conglomeration of wolves one wants to consider for a particular reason. For example, in the Yellowstone Wolf Reintroduction Environmental Impact Statement (USFWS 1994b, 6–66), the following operational definition of a wolf population was adopted: "A wolf population is at least 2 breeding pairs of wild wolves successfully raising at least 2 young each (until December 31 of the year of their birth), for 2 consecutive years in an experimental area."

Studies of wolf population dynamics cover wolf density and distribution, population composition, the rates of births, deaths, and dispersal of wolves, and in particular, the means by which these parameters vary and change and the factors that affect them. Numerous scientific and popular articles and books deal with wolves, and most cover some aspects of wolf population dynamics. Several recent works have made important points concerning wolf conservation (e.g., Peek et al. 1991; Fritts et al. 1994; Fritts and Carbyn 1995; Mech 1995a), and central to all of them is information on wolf populations.

Since Mech's (1970) comprehensive summary of wolf biology, thousands of wild wolves have been radio-collared and monitored intensively (Mech 1995e), and many others have been studied in captivity (Frank 1987). These studies have allowed the collection of information

critical to understanding wolf population dynamics. Radio-tracking has not only helped produce better data on wolf population size and trends, but has also yielded important new data about wolf mortality and survival, birth rates, and dispersal. In addition, radio-tracking studies have shed much light on wolf interactions with their prey, another key to understanding wolf population dynamics (Nelson and Mech 1981; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987, 1997; Fuller 1990; Mech et al. 1998).

In 1983, Keith suggested that four factors dominate wolf population dynamics: wolf density, ungulate density, human exploitation, and ungulate vulnerability. Subsequent studies of wolf population dynamics (e.g., Fuller 1989b, 1995b) show that to understand wolf population ecology and conservation in a general way, we can reduce these factors to three key elements: food, people, and source populations. These are complex elements, to be sure, but they are clearly the most important to understand.

The abundance and availability of food (i.e., hoofed prey such as red deer or moose; see Peterson and Ciucci, chap. 4, and Mech and Peterson, chap. 5 in this volume) determine the potential for wolves to inhabit areas. Given higher ungulate populations, wolves should have more opportunities to catch prey, and food accessibility ultimately affects nutritional levels and thus wolf reproduction, survival, and behavior (Mech 1970; Van Ballenberghe et al. 1975; Zimen 1976; Packard and Mech 1980; Keith 1983; Mech et al. 1998). Prey accessibility is related not only to the abundance, but also to the vulnerability of prey (Mech 1970; Peterson and Page 1988; Mech et al. 1998; Peterson et al. 1998). Deep snow, age, or disease may make some prey more vulnerable, and thus more "accessible," than others (see Mech and Peterson, chap. 5 in this volume).

Second, human behaviors that result in the direct or indirect killing of wolves may influence where wolves live and in what numbers. In designated wilderness areas, national parks, and wildlife refuges, wolves are generally protected from human-related deaths. Wolf populations also seem little affected by snowmobiles, vehicles, logging, mining, and other human activities outside of these areas (Thiel et al. 1998; Merrill 2002), except as these factors facilitate accidental or intentional killing by humans or change prey density (e.g., logging). Even then, once a wolf population is large enough, such human take of wolves affects the population level little (see below) except along the frontier of the wolf's range.

In the past, of course, adverse human attitudes and traditions played a significant role in reducing wolf populations, especially in North America and western Europe when extensive poisoning and deliberate government persecution were applied (Young and Goldman 1944; Boitani 1995). In much of eastern Europe and Asia today, human attitudes toward wolves are still important determinants of wolf killing and hence population trends. Poland, for example, is experiencing its second wolf population resurgence in the last century (fig. 6.1) as a result of more tolerant public attitudes (Okarma 1992).
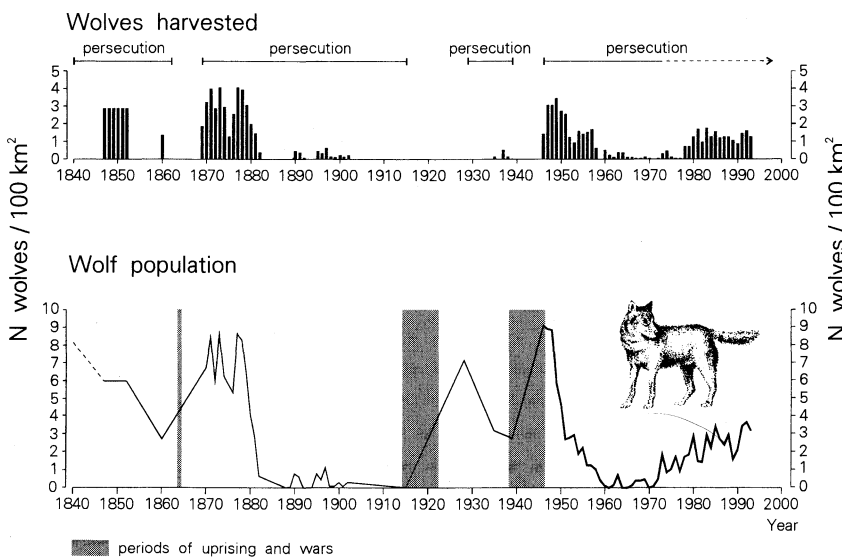
FIGURE 6.1. Long-term dynamics of wolf hunting harvest and wolf density in Bialowieza Primeval Forest (BPF), Poland, 1847–1993. Thin line, density reconstructed based on regression between numbers shot and population size between 1946 and 1971. Thick line, density determined by snow tracking surveys; numbers recorded in the exploited forests of the Polish part and in the Belarusian part of BPF were summed. Wolves recorded in Bialowieza National Park (BNP) were not added (with the exception of 1961, when wolves were recorded in BNP only) because they were most likely already counted in either of the two parts. (From Jedrzejewska et al. 1996.)

Finally, source populations of wolves are crucial to the establishment of new populations and to the maintenance of populations that are heavily controlled or harvested. For example, wolf populations in marginal habitats (i.e., where food resources are poor or human-caused mortality is high) are often successfully augmented by dispersal from adjacent source populations (Mech 1989; Lariviere et al. 2000). This is also true for small populations within larger regions of wolf abundance (Hayes and Harestad 2000a). Wolves are great dispersers and can move to new areas fairly easily (see Mech and Boitani, chap. 1 in this volume, and below). Thus, the distance of one wolf population from the next nearest one plays yet another primary role in wolf population ecology (Wydeven et al. 1995).

Below we try to summarize and synthesize what is known about wolf populations and the way they behave. We draw on data from perhaps the most comprehensive set of population literature there is for a large mammal to detail how various factors interact to affect wolf population dynamics. We will begin by looking at the bigger picture of how wolf populations are distributed geographically and by examining the role of packs in population change. Then we will continue through discussions of wolf density and how variables such as food affect it; the critical factors of reproduction, survival, mortality, and dispersal; rates of wolf population change; natural regulation of wolf populations; the role of cumulative effects on populations; and how well wolf populations persist. We conclude by assessing future needs for studying wolf population dynamics.

Wolf Distribution

Large-Scale Patterns

Historically, wolves occupied every habitat containing large ungulates in the Northern Hemisphere from about 20° N latitude (mid-Mexico, southern Saudi Arabia, and India) to the polar ice pack (Young and Goldman 1944). Vegetation type makes little difference to wolves as long as populations of hoofed prey are available. Wolves inhabit deserts, prairies, woodlands, swamps, tundra, and "barren lands" from sea level to mountaintops.

In general, wolves are very adaptable: they enter towns or villages at night (Zimen and Boitani 1979), cross four-lane highways and open landscapes (Merrill and Mech 2000), and den near logging sites, open-pit mines, garbage dumps, and military firing ranges (Thiel et al. 1998; Merrill 2002). They have few, if any, natural predators

(see Ballard et al., chap. 10 in this volume), but persecution of wolves by humans, primarily by poisoning, long ago eliminated wolves from many portions of their historical range (see Fritts et al., chap 12, and Boitani, chap. 13 in this volume).

Minimum Spatial Requirements

Wolf distribution on a small scale is limited mostly by the amount of land available containing enough prey with high enough productivity to support at least one pack. Even at the highest imaginable average prey densities (e.g., a biomass equal to 15 deer or 3 moose/km^2), it would seem that an individual pack of four wolves probably requires a territory of about 75 km^2 (30 mi^2) to meet its nutritional requirements (see fig. 6.2; see also Peterson and Ciucci, chap. 4, and Kreeger, chap. 7 in this volume). Few territories that small have been documented outside of small islands, although a pack of six wolves in 39 km^2 (15 mi^2) has been recorded in northeastern Minnesota (L. D. Mech and S, Tracy, unpublished data). Mean territory sizes of wolf packs on the mainland whose major prey occur at the highest measured densities (equivalent to 7–10 deer/km^2) actually average 100–200 km^2 (39–78 mi^2) (see below). In places where prey are at very low densities, average pack territories may measure more than 1,000 km^2 (390 mi^2) each (Mech 1988a; Mech et al. 1998).

An important consideration regarding the minimum area required by a wolf population is that a single, isolated pack should have a lower chance of persisting than a group of several adjacent packs. Theoretically, the chances of an isolated pack avoiding some catastrophe or difficulties from inbreeding vary inversely with its distance or degree of isolation (e.g., distance to a natural travel corridor) from the next nearest pack or packs (see the section on dispersal below). However, with an abundant food supply and no human-caused deaths, a population of 12–50 wolves on Isle Royale resulting from a single pair survived for 50 years (Peterson 2000), even after having lost an estimated 50% of its genetic variability (Wayne et al. 1991).

Nevertheless, if we were prescribing a formula for the smallest demographically viable wolf population, we might include two to three adjacent packs (cf. USFWS 1992, 18) of four wolves each, 40–60 km (24–36 mi) from other wolves. At average ungulate densities (e.g., 8 deer/km^2), pack territories might each cover 300 km^2 (117 mi^2). Such a population could persist anywhere

ungulate prey occurred at the specified biomass density and at reasonable productivity, and where wolf mortality was less than net reproduction.

Studies of several small wolf populations add insight to this question. In the wildlife reserves of Quebec, human harvesting of wolves averaged 2–74% of the populations annually; populations persisted in reserves larger than 1,500 km² (585 mi²), but tended to be unstable in smaller reserves (Lariviere et al. 2000). This finding was similar to that in Poland's 1,538 km² (600 mi²) Bieszczady National Park, with a population of 26–33 wolves in five packs (Smietana and Wajda 1997).

Packs

Wolf populations are composed of packs and lone wolves, but as indicated earlier, packs form the basic units of a population. Most lone wolves are only temporarily alone as they disperse from packs and either start their own packs or join existing packs (see Mech and Boitani, chap. 1 in this volume, and below).

Origin of Packs

Packs originate when a male and female wolf meet, pair up, and produce pups (Rothman and Mech 1979). There are many variations on this method of pack formation and pack maintenance, but basically packs are composed of a mated pair of wolves and their offspring (see Mech and Boitani, chap. 1 in this volume).

Pack Size and Composition

Packs vary in size from two to forty-two wolves (table 6.1) (Rausch 1967; Fau and Tempany 1976, cited in Carbyn et al. 1993), and average pack sizes range from three to eleven. As indicated by Mech and Boitani in chapter 1 in this volume, the size of a given pack can vary by many multiples of the basic founding pair. Furthermore, when prey availability is reduced, large packs can be reduced in size through lower reproduction and/or survival or through dispersal. In addition, as packs enlarge, they sometimes split or proliferate. Therefore, we do not view pack size as a serious constraint on wolf population increases or decreases, but change in pack size is one of the primary mechanisms through which wolf population size changes (Rausch 1967).

Pack size does not necessarily differ among wolf populations whose major prey are different. That is, average sizes of wolf packs feeding mainly on moose are not larger than those of packs feeding on deer, although mean pack sizes for those feeding on caribou and elk are larger than for those feeding on deer or moose (see table 6.1) (but also see Mech and Boitani, chapter 1 in this volume). Pack size also does not vary with relative prey biomass; packs are just as large at high prey densities as they are at low prey densities (tables 6.1 and 6.2).

Seasonal Changes in Pack Size

Packs are obviously largest just after pups are born; this is the major annual increment to wolf populations. As summer progresses, some pups and a few adults die, reducing overall pack size, and mortality of adults typically peaks during fall and winter (see below). Fall and winter are also major times of wolf dispersal, so pack sizes diminish further as members leave. However, a few wolves also join packs, single wolves pair with others, and young wolves often make predispersal trips away from packs for periods of days to months (see Mech and Boitani, chap. 1 in this volume). Thus pack sizes can fluctuate through the year.

"Observed" pack sizes may seem to follow a somewhat different pattern than outlined above, because during summer pack members more often travel alone. Pack members are more often together during winter, but even then packs may split apart for days to weeks before getting together again (see Mech and Boitani, chap. 1 in this volume). Thus most studies estimate pack sizes from the maximum number of wolves observed in a pack during winter, as recommended by Mech (1973, 1982b).

Pack Composition

In most wolf packs, pups, or young-of-the-year, form the single largest age class, followed by yearlings. Some packs may include one or more 2- or 3-year-olds. These wolves are usually all offspring of the breeding pair. Some packs also contain a postreproductive female or a wolf "adopted" from another pack (see Mech and Boitani, chap. 1 in this volume). Wolf packs in national parks such as Denali (Mech et al. 1998) and Yellowstone (Bangs et al. 1998), where human-related mortality is minimal, usually typify this type of age composition.

Where wolves are subject to human taking, estimates of pack composition in midwinter indicate that adults and yearlings usually constitute 54–76% of all pack

TABLE 6.1. Estimated early- to midwinter size and composition of wolf packs and proportion of nonresident wolves in various populations

Location	Main prey	Pack size[a]			% adults and yearlings[b]	Percent non-residents	Reference
		Mean	Maximum	N			
Northern Wisconsin	Deer	3.6	—	46	—	—	Wydeven et al. 1995 (1985–1991)
Northwestern Minnesota	Deer	4.3	9	24	—	14	Fritts and Mech 1981
Voyageurs Park, Minnesota	Deer	5.5	11	23	—	10	Gogan et al. 2000
Southern Quebec	Deer	5.6	10	19	—	—	Potvin 1988
East-central Ontario	Deer	5.9	9	54	69	20	Pimlott et al. 1969
Algonquin Park, Ontario	Deer	6.0	13	44	—	—	Forbes and Theberge 1995
North-central Minnesota	Deer	6.0	8	4	—	—	Berg and Kuehn 1982
North-central Minnesota	Deer	6.7	12	33	54(54)[c]	7	Fuller 1989b
Northeastern Minnesota	Deer	7.2	10	11	58(50)[c]	—	Van Ballenberghe et al. 1975
West-central Yukon	Sheep	4.6	8	5	—	—	Sumanik 1987
Northwestern Alaska	Caribou	8.6	24	34	—	—	Ballard et al. 1997
Northern Alaska	Caribou	9.5	15	12	—	—	Dale et al. 1995
Southwestern Manitoba	Elk	8.4	16	13	—	—	Carbyn 1980
Central Rocky Mts, MT, BC	Elk	10.7	19	38	—	—	Boyd and Pletscher 1999
Jasper Park, Alberta	Elk	11.5	14	4	—	—	Carbyn 1974
Southwestern Quebec	Moose	3.7	6	16	—	9	Messier 1985a,b (low prey area)
Pukaskwa Park, Ontario	Moose	3.8	7	39	—	—	Bergerud et al. 1983
Southwestern Quebec	Moose	5.7	8	11	—	9	Messier 1985a,b (high prey area)
Southern Yukon	Moose	5.8	25	103	66(55)[c]	10	Hayes et al. 1991
Northwestern Alberta	Moose	6.0	12	22	76	12	Bjorge and Gunson 1989
East-central Yukon	Moose	6.8	20	146	—	—	Hayes and Harestad 2000b
South-central Alaska	Moose	7.5	20	59	—	—	Ballard et al. 1987
Northeastern Alberta	Moose	7.6	7	7	60	13	Fuller and Keith 1980a (both study areas)
Denali Park, Alaska	Moose	8.9	29	91	57	—	Mech et al. 1998
Kenai Peninsula, Alaska	Moose	9.8	29	32	65	—	Peterson, Woolington, and Bailey 1984
Northern Alberta	Bison	8.4	14	20	—	—	Carbyn et al. 1993
Isle Royale, all years							
Isle Royale, Michigan	Moose	5.8	22	135	75[d]	—	Mech 1966b; Jordan et al. 1967; Peterson 1977; Peterson and Page 1988; Peterson et al. 1998; R. O. Peterson, personal communication (1959–1994)
Isle Royale, by wolf trend							
Isle Royale, Michigan	Moose	4.4	11	39	—	—	Peterson and Page 1988; Peterson et al. 1998; R. O. Peterson, personal communication (1983–1994)
Isle Royale, Michigan	Moose	7.8	18	37	—	—	Peterson 1977; Peterson and Page 1988 (1973–1980)

(continued)

TABLE 6.1 *(continued)*

Location	Main prey	Pack size[a]			% adults and yearlings[b]	Percent non-residents	Reference
		Mean	Maximum	N			
Isle Royale, Michigan	Moose	6.2	22	46	—	—	Mech 1966b; Jordan et al. 1967; Peterson 1977; R. O. Peterson, personal communication (1959–1972)
Isle Royale, Michigan	Moose	3.9	—	21	—	—	Peterson and Page 1988 (1980–1982)
Isle Royale by ~stable biomass index							
Isle Royale, Michigan	Moose	6.5	—	34	—	—	Peterson 1977; Peterson and Page 1988; R. O. Peterson, personal communication (1968–1976)
Isle Royale, Michigan	Moose	3.1	—	18	—	—	Peterson et al. 1998; R. O. Peterson, personal communication (1987–1991)
Isle Royale, Michigan	Moose	4.7	—	30	—	—	Peterson and Page 1988 (1980–1985)
Isle Royale, Michigan	Moose	7.4	—	24	—	—	Mech 1966b; Jordan et al. 1967; R. O. Peterson, personal communication (1959–1966)
Northeastern Minnesota, all years							
Northeastern Minnesota	Deer	5.8	15	198	—	16	Mech 1986 (1967–1985)
Northeastern Minnesota by wolf/deer trend							
Northeastern Minnesota	Deer	6.5	—	—	—	—	Mech 1986 (1967–1970)
Northeastern Minnesota	Deer	6.2	—	—	—	—	Mech 1986 (1971–1975)
Northeastern Minnesota	Deer	5.2	—	—	—	—	Mech 1986 (1976–1984)

Summary and statistical test results
Average pack size and principal prey species

Species	Deer	Moose	Elk	Caribou
No. studies	10	11	3	2
Mean pack size	5.66	6.49	10.2	9.05

Two-sample, two-tailed *t* tests assuming equal variance

Test	d.f.	P	t
Deer vs. moose	19	.24	−1.22
Deer vs. elk	11	< .001	−5.89
Deer vs. caribou	10	.002	−4.31
Moose vs. elk	12	.01	−3.08

Biomass index/wolf and % adults + yearlings in the fall population: $r^2 = .25$; d.f. = 8; $P = .17$.

[a]Including all groups ≥2 wolves.

[c]Percentage of females within age class.

[b]Percentage of wolves ≥1 year old in the population.

[d]Average percentage of wolves ≥1 year old in the fall when the population was stable between 1971 and 1995 (Peterson et al. 1998).

TABLE 6.2. Mean ungulate and wolf densities and ungulate biomass/wolf ratios during winter in North America

| Location | Years | Prey species | Number/1,000 km² | | Wolves | Ungulate biomass index per wolf | Reference(s) |
			Ungulates	Ungulate biomass index[a]			
Northeastern Minnesota	1970–1971	Deer	5,100	9,900	42	236	Van Ballenberghe et al.
		Moose	800				1975
Voyageurs Park, Minnesota	1987–1991	Deer	8,370	9,150	33	277	Gogan et al. 2000
		Moose	130				
Southwestern Manitoba	1975–1978	Elk	1,200	8,740	26	336	Carbyn 1980, 1983b
		Moose	800				
		Deer	340				
Northwestern Alberta	1975–1980	Moose	1,165	7,332	24	306	Bjorge and Gunson 1989
		Elk	114				
Northern Wisconsin	1986–1991	Deer	7,200	7,200	18	400	Wydeven et al. 1995
Northwestern Minnesota	1972–1977	Deer	5,000	6,800	17[b]	400	Fritts and Mech 1981
		Moose	300				
East-central Ontario	1958–1965	Deer	5,769	6,645	38	175	Pimlott et al. 1969
		Moose	146				
Southern Quebec	1980–1984	Deer	3,000	6,600	28	236	Potvin 1988
		Moose	600				
North-central Minnesota	1980–1986	Deer	6,160	6,280	39	161	Fuller 1989b
		Moose	20				
North-central Minnesota	1978–1979	Deer	6,170	6,170	10	617	Berg and Kuehn 1980
Northeastern Minnesota	1946–1953	Deer	3,475	5,791	23	252	Stenlund 1955
		Moose	386				
Kenai Peninsula, Alaska	1976–1981	Moose	800	4,826	14	345	Peterson, Woolington,
		Caribou	13				and Bailey 1984
South-central Alaska	1945–1982	Moose	665	4,612	7[c]	659[c]	Ballard et al. 1987;
		Caribou	311				Davis 1978
Algonquin Park, Ontario	1969	Deer	3,100	4,024	36	112	Kolenosky 1972;
		Moose	154				Pimlott et al. 1969
Jasper Park, Alberta	1969–1972	Elk	500	2,730	8	364	Carbyn 1974
		Sheep	470				
		Goat	120				
		Moose	80				
		Deer	80				
		Caribou	40				
Algonquin Park, Ontario	1988–1992	Deer	395	2,615	27	97	Forbes and Theberge
		Moose	370				1995
East-central Yukon	1989–1994	Moose	353	2,609	6[c]	435[c]	Hayes and Harestad
		Caribou	238				2000a,b
		Goat	11				
		Sheep	4				
Northern Alaska	1989–1990	Caribou	510	2,240	7	320	Adams and Stephenson
		Moose	120				1986; Singer 1984;
		Sheep	500				Dale et al. 1995
Southwestern Quebec	1980–1984	Moose	370	2,200	14	159	Messier 1985a,b
							(high prey area)

TABLE 6.2 (continued)

Location	Years	Prey species	Number/1,000 km²		Wolves	Ungulate biomass index per wolf	Reference(s)
			Ungulates	Ungulate biomass index[a]			
Denali Park, Alaska	1966–1974	Moose	164	2,002	6	334	Haber 1977
		Sheep	478				
		Caribou	270				
Pukaskwa Park, Ontario	1975–1979	Moose	296	1,789	12	149	Bergerud et al. 1983
		Caribou	13				
Interior Alaska	1975–1978	Moose	206	1,560	9	173	Gasaway et al. 1983
		Caribou	162				
Southern Yukon	1983–1988	Moose	207	1,556	8[c,d]	207[c,d]	Hayes et al. 1991
		Sheep	260				
		Caribou	27				
		Goats	29				
Denali Park, Alaska	1986–1992	Caribou	300	1,531	6	255	Meier et al. 1995
		Moose	133				
		Sheep	133				
Southwestern Quebec	1980–1984	Moose	230	1,380	8	173	Messier 1985a,b (low prey area)
Northwestern Alaska	1987–1991	Moose	166	1,324	5	267	Ballard et al. 1997
		Caribou	164				
Northern Alberta	1979	Bison	153	1,224	8	152	Oosenbrug and Carbyn 1982
West-central Yukon	1985–1986	Moose	62	1,143	7	153	Sumanik 1987
		Caribou	45				
		Sheep	681				
Northeastern Alberta	1975–1977	Moose	180	1,114	6	186	Fuller and Keith 1980a,b, Gunson 1995 (AOSERP area)
		Caribou	17				
Denali Park, Alaska	1984–1985	Moose	94	865	3	288	Singer and Dalle-Molle 1985
		Caribou	106				
		Sheep	89				
Isle Royale, all years							
Isle Royale, Michigan	1959–1994	Moose	2,096	12,576	44	286	Mech 1966b; Jordan et al. 1967; Peterson 1977; Peterson and Page 1988; Peterson et al. 1998; R. O. Peterson, personal communication
Isle Royale by wolf trend							
Isle Royale, Michigan	1983–1994	Moose	2,399	14,394	31	465	Peterson and Page 1988; Peterson et al. 1998; R. O. Peterson, personal communication
Isle Royale, Michigan	1973–1980	Moose	2,247	13,482	71	190	Peterson 1977; Peterson and Page 1988

TABLE 6.2 *(continued)*

Location	Years	Prey species	Number/1,000 km²				Reference(s)
			Ungulates	Ungulate biomass index[a]	Wolves	Ungulate biomass index per wolf	
Isle Royale, Michigan	1959–1972	Moose	1,844	11,064	41	270	Mech 1966b; Jordan et al. 1967; Peterson 1977; R. O. Peterson, personal communication
Isle Royale, Michigan	1980–1982	Moose	1,485	8,910	58	154	Peterson and Page 1988
Isle Royale, by ~stable biomass indicator							
Isle Royale, Michigan	1968–1976	Moose	2,678	16,068	49	328	Peterson 1977; Peterson and Page 1988; R. O. Peterson, personal communication
Isle Royale, Michigan	1987–1991	Moose	2,558	15,348	25	614	Peterson et al. 1998; R. O. Peterson, personal communication
Isle Royale, Michigan	1980–1985	Moose	1,490	8,940	51	175	Peterson and Page 1988;
Isle Royale, Michigan	1959–1966	Moose	1,321	7,926	50	158	Mech 1966b; Jordan et al. 1967; R. O. Peterson, personal communication
Northeastern Minnesota, all years							
Northeastern Minnesota	1967–1993	Moose[e] Deer[e]	560 1,212	4,572	28	163	Mech 1973, 1986; Mech and Nelson 2000; Peek et al. 1976; Fuller 1989b
Northeastern Minnesota by wolf/deer trend							
Northeastern Minnesota	1967–1970	Moose[e] Deer[e]	600 3,380	6,980	38	186	Mech 1973, 1986; Peek et al. 1976; Fuller 1989b
Northeastern Minnesota	1971–1975	Moose[e] Deer[e]	570 1,800	5,220	33	161	Mech 1973, 1986; Mech and Nelson 2000; Peek et al. 1976; Fuller 1989b
Northeastern Minnesota	1976–1984	Moose[e] Deer[e]	550 600	3,900	23	170	Mech and Nelson 2000; Peek et al. 1976; Fuller 1989b

Summary and statistical test results

Test	r^2	d.f.	P	Regression
BMI/wolf and mean pack size	.06	24	.23	
Total BMI and mean pack size	.004	24	.76	
Total BMI and mean density	.64	31	< .001	$y = 3.5 + 3.27x$

TABLE 6.2 *(continued)*

	BMI / wolf summary statistics
Mean	271
SE	23
SD	131
Range	97–659
No. studies	32

Source: Adapted from Keith 1983; Fuller 1989b.

[a]Relative biomass values were assigned as follows (similar to Keith 1983); bison, 8; moose, 6; elk, 3; caribou, 2; bighorn sheep, 1; Dall sheep, 1; mountain goat, 1; mule deer, 1; white-tailed deer, 1.

[b]Wolf population newly protected and expanding.   [c]Wolf population heavily exploited.   [d]Wolf population recovering from heavy exploitation.

[e]Ungulate densities extrapolated between estimates for 1970 (Peek et al. 1976) and 1975 (Fuller 1989b), then assumed constant after 1975.

members (see table 6.1). The limited data do not indicate any particular bias in sex ratios of adults and yearlings; there is either an equal sex ratio or one slightly biased toward females (Mech 1970).

Populations with the highest proportion of pups in packs are usually those whose numbers have been reduced substantially through control efforts, thus leaving only small packs or pairs. When these groups produce an average litter of pups (4–6; see below), surviving pups can clearly make up a high proportion of the pack. Similarly, populations of wolves recolonizing areas have ample opportunity to form new packs made up of only a pair of wolves, so newborn pups form a large part of populations in such areas.

Lone Wolves

At any given time, some wolves that have dispersed from packs are traveling alone. These wolves may be either temporarily away from their pack or permanently dispersed and looking for mates. The proportion of these nonresident wolves in a population probably varies seasonally, as do dispersal rates and the rates at which individuals settle into territories (see Mech and Boitani, chap. 1 in this volume), but a variety of studies have documented or surmised that these wolves compose about 10–15% of a wolf population in winter on average (see table 6.1).

Density

Variation

Wolf densities naturally vary tremendously. It is common for studies in the far north to record healthy wolf populations with densities of less than $5/1,000$ km^2

$(391$ $mi^2)$ (see table 6.2), whereas on Isle Royale in Lake Superior (Canada-U.S. border) wolf density reached $92/1,000$ km^2 in 1980 (Peterson and Page 1988). Furthermore, studies of wolf density have varied in the precise methods used to derive the area involved, so often their results are not strictly comparable (Burch 2001). In general, however, maximum midwinter wolf densities documented for mainland populations over a number of years have rarely measured more than $40/1,000$ km^2 (see table 6.2).

Pimlott (1967) suggested 30 years ago that some intrinsic control on wolf numbers limited density to a maximum of about 40 wolves/$1,000$ km^2 in most areas. This conclusion was based on his own observations in Algonquin Provincial Park in Ontario, Canada, and on limited observations of others. Mech (1973) concurred with this assessment, but noted exceptions where prey densities were extremely high. In addition to the findings on Isle Royale noted above, Fuller (1989b) recorded maximum densities in north-central Minnesota during the 1980s of 69 wolves/$1,000$ km^2 in early winter and $50/1,000$ km^2 in late winter. The work of Peterson and Page (1988) on Isle Royale, and the evidence presented by Keith (1983), convinced Peterson and Page (1988) that the ultimate limit on wolf density is that imposed by food, as many other workers had also concluded (Mech 1970; Van Ballenberghe et al. 1975; Packard and Mech 1980; Keith 1983).

Food

In fact, 64% of the variation in wolf density in all North American studies was directly accounted for simply by variation in prey biomass. This relationship (Keith 1983; Fuller 1989b) is now based on thirty-one intensive stud-
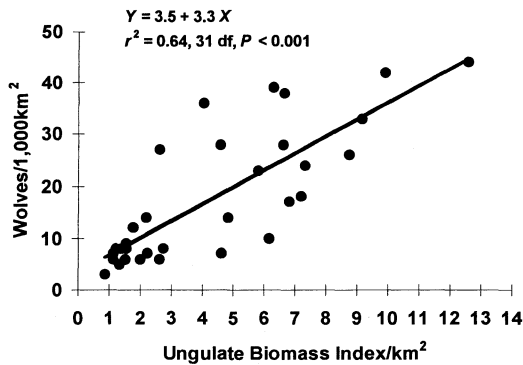
FIGURE 6.2. Relationship between ungulate biomass index and wolf density, plotted from data in table 6.2. (Adapted from Keith 1983 and Fuller 1989b.)

ies that measured total average ungulate biomass (often more than one prey species) and average wolf populations for a period of several years (see table 6.2). The relationship between prey abundance and wolf numbers may vary for areas with migratory versus nonmigratory prey, or where prey concentrate seasonally. However, there are no indications that, over time, wolf numbers are mainly limited by anything other than food (usually ungulate numbers and accessibility), given the above considerations. A plot of the relationship between food abundance (i.e., ungulate biomass index; see table 6.2) and wolf density (fig. 6.2) does not "level off," and thus suggests that even at prey densities higher than have been recorded thus far, this relationship should be valid.

Effect of Long-Term Mortality

The actual ungulate biomass index per wolf varies among studies (mean = 271; median = 254; range = 97–659; see table 6.2), as indicated by the deviation of data points from the regression line in figure 6.2. This ratio, however, is highest for heavily exploited (Peterson, Woolington, and Bailey 1984; Ballard et al. 1987; Hayes and Harestad 2000a,b) and newly protected wolf populations (e.g., Berg and Kuehn 1980; Fritts and Mech 1981; Wydeven et al. 1995), and lowest for unexploited wolf populations (Oosenbrug and Carbyn 1982; Bergerud et al. 1983) and those where ungulates are heavily harvested (Kolenosky 1972).

It seems clear that newly protected wolf populations would have the potential to grow until food was a limiting factor; thus the relative number of ungulates initially and for some time would be high. In addition, it

also makes some sense that perpetually harvested wolf populations, despite compensatory reproduction, might never "catch up" with prey densities and thus would fail to achieve some maximum density. Gasaway et al. (1992, 39) demonstrated for numerous regions in Alaska that wolf populations that they believed were limited by harvesting occurred at much lower densities in relation to prey availability than did populations that were lightly harvested.

Conversely, completely unexploited or completely protected wolf populations are probably making the most of their food supply and achieving the highest densities possible. This should be especially true where, in addition, ungulates are harvested by humans, thus holding their numbers low.

Over the long run, however, we would expect that the average ratio of wolves to ungulate biomass in a system unaffected by humans might reach some median value that reflects the bioenergetic balance of predator and prey. In fact, Isle Royale's unexploited population seems to have done just that; the mean ungulate biomass per wolf there over a 36-year period was 286, almost identical to the mean for all areas (see table 6.2).

The relationship between food or prey density and wolf density is sufficiently strong that, given specific conditions, one can make reasonable predictions concerning the average density of wolves. For example, a lightly to moderately harvested wolf population whose only prey is moose occurring at a density of $1/km^2$ (6 "deer-equivalents"/km^2) would probably have a density of 23 ($\pm$ 5 SE) wolves/1,000 km^2. As will be discussed below, however, other factors determine the specific wolf numbers and population trends in various areas.

Temporal Variation

Changes in wolf density due to varying prey density have been documented by long-term studies in northeastern Minnesota (Mech 1977b, 1986, 2000c) and on Isle Royale (Peterson et al. 1998), in areas of varying moose density in southwestern Quebec (Messier and Crête 1985), and in Denali National Park, Alaska (Mech et al. 1998). The numerical response of an individual wolf population to a change in food supply or prey biomass may be like that for other cyclic mammals (Peterson, Page, and Dodge 1984), and thus for any one year, the ratio of prey biomass to wolves may differ from other years and from other areas in the same year. When ungulate numbers fluctuate from year to year, changes in wolf density may

lag for up to several years in a single-prey system (Mc-Laren and Peterson 1994); we will discuss the reason for this finding below. In multi-prey systems, wolf numbers may respond more quickly to changes in prey vulnerability (Mech et al. 1998; see below).

Wolf densities also vary where wolves are heavily harvested, have the opportunity to recover from overharvest, or are newly protected. In some areas wolves have been intentionally harvested more heavily in one or more years to reduce their effect on prey populations (e.g., Ballard et al. 1987; Bjorge and Gunson 1983; Gasaway et al. 1983; Hayes and Harestad 2000a), and their numbers have declined precipitously. Conversely, some of these same populations have then been allowed to recover, and their numbers have increased to a similar degree (e.g., Bjorge and Gunson 1989; Hayes and Harestad 2000a). In other cases, wolves have recolonized areas from which they were extirpated many years earlier, and these populations, too, have increased rapidly (e.g., Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Wydeven et al. 1995; see below).

Territory Size

Wolves usually occupy exclusive, defended territories, although there are several exceptions to this generaliza-tion (see Mech and Boitani, chap. 1 in this volume). Territoriality is generally thought to help stabilize population dynamics by tightening the feedback loop to local resources. This theory has not been tested in wolf populations. About all we can add to this discussion is that, as indicated above and by Mech and Boitani (chap. 1 in this volume), wolf pack sizes adjust considerably to food supply or vulnerable prey biomass within territories, but factors affecting prey vulnerability, such as winter severity, usually are pervasive across many territories.

Wolf pack territory sizes vary, on average, fourteen-fold among areas (table 6.3). Average territory size and, more particularly, the average area per wolf vary most directly with food resources or prey abundance, as well as with prey type and the mean annual rate of population change. On average, about 33% of the variation in mean territory size ($r^2 = .33$, $P < .001$, d.f. = 32) and 35% of that in mean territory area per wolf ($r^2 = .35$, $P < .001$, d.f. = 32) can be attributed to variation in prey biomass; in general, the higher the prey density, the smaller the territory (table 6.3). In Wisconsin, a similar relationship ($r^2 = .59$; $P < .01$) has been documented for individual wolf territories and their corresponding deer densities (Wydeven et al. 1995).

However, territory sizes still vary considerably, even among areas where total prey biomass is about the same.

TABLE 6.3. Ungulate biomass index, mean territory size, mean pack size in winter, and mean territory area per wolf for wolf populations utilizing different primary prey

Primary prey	Location	Ungulate biomass index[a]	Territory size (km²) $\bar{x}$	N	Pack size	Territory area per wolf (km²)	Finite rate of increase	Reference
Deer	Northeastern Minnesota	9,900	143	11	7.2	20	—	Van Ballenberghe et al. 1975
Deer	Voyageurs Park, Minnesota	9,150	152		5.5	28	—	Gogan et al. 2000
Deer	Northern Wisconsin	7,200	176	41	3.5	50	1.16	Wydeven et al. 1995 (1986–1991)
Deer	Northwestern Minnesota	6,800	344	8	4.6	80	1.13	Fritts and Mech 1981
Deer	Algonquin Park, Ontario	6,645	259	47	5.9	25	—	Pimlott et al. 1969
Deer	Southern Quebec	6,600	199	21	5.6	36	—	Potvin 1988
Deer	North-central Minnesota	6,280	116	33	5.7	20	1.02	Fuller 1989b
Deer	North-central Minnesota	6,170	230	4	6.0	46	—	Berg and Kuehn 1980, 1982
Deer	Algonquin Park, Ontario	4,024	224	1	8.0	28	—	Kolenosky 1972
Deer	Algonquin Park, Ontario	2,615	149	44	6.0	25	1.01	Forbes and Theberge 1995
Sheep	West-central Yukon	1,143	754	5	4.6	164	—	Sumanik 1987
Elk	Southwestern Manitoba	8,740	293	12	8.4	35	0.86	Carbyn 1980, 1983b
Moose	Northwestern Alberta	7,332	424	9	6.0	71	1.29	Bjorge and Gunson 1989

TABLE 6.3 *(continued)*

Primary prey	Location	Ungulate biomass index[a]	Territory size (km²)		Pack size	Territory area per wolf (km²)	Finite rate of increase	Reference
			$\bar{x}$	N				
Moose	Kenai Peninsula, Alaska	4,826	638	18	11.2	57	1.03	Peterson, Woolington, and Bailey 1984
Moose	South-central Alaska	4,612	1,645	—	7.5	219	0.88	Ballard et al. 1987
Moose	East-central Yukon	2,609	1,478	17	6.8	217	1.49	Hayes and Harestad 2000a,b
Moose	Southwestern Quebec	2,220	397	14	5.7	68	1.06	Messier 1985a,b (high prey area)
Moose	Interior Alaska	2,080	665	—	9.3	72	0.76	Gasaway et al. 1992 (1972–1975)
Moose	Pukaskwa Park, Ontario	1,789	250	—	2.8	89	0.84	Bergerud et al. 1983
Moose	Southern Yukon	1,556	1,192	—	5.5	193	0.97	Hayes et al. 1991
Moose	Denali Park, Alaska	1,531	1,330	15	8.9	133	1.20	Mech et al. 1998
Moose	Southwestern Quebec	1,380	255	16	3.7	69	1.11	Messier 1985a,b (low prey area)
Moose	Northwestern Alaska	1,324	1,372	14	9.0	152	0.88	Ballard et al. 1997
Moose	Northeastern Alberta	1,114	834	7	7.7	110	1.21	Fuller and Keith 1980a (AESORP area)
Bison	Northern Alberta	1,224	1,352	3	12.3	110	—	Carbyn et al. 1993; Oosenbrug and Carbyn 1982
Isle Royale, all years								
Moose	Isle Royale, Michigan	12,576	145	135	5.8	25	1.00	Mech 1966b; Jordan et al. 1967; Peterson 1977; Peterson and Page 1988; Peterson et al. 1998; R. O. Peterson, personal communication (1959–1994)
Isle Royale by wolf trend								
Moose	Isle Royale, Michigan	14,400	167	39	4.4	38	0.97	Peterson and Page 1988; Peterson et al. 1998; R. O. Peterson, personal communication (1983–1994)
Moose	Isle Royale, Michigan	13,480	118	37	7.8	15	1.11	Peterson 1977; Peterson and Page 1988 (1973–1980)
Moose	Isle Royale, Michigan	11,070	166	46	6.2	27	1.01	Mech 1966b; Jordan et al. 1967; Peterson 1977; R. O. Peterson, personal communication (1959–1972)
Moose	Isle Royale, Michigan	8,910	78	21	3.9	20	0.42	Peterson and Page 1988 (1980–1982)
Isle Royale by ~stable BMI periods								
Moose	Isle Royale, Michigan	16,070	144	34	6.5	22	1.09	Peterson 1977; Peterson and Page 1988; R. O. Peterson, personal communication (1968–1976)

(continued)

TABLE 6.3 *(continued)*

Primary prey	Location	Ungulate biomass index[a]	Territory size (km²)		Pack size	Territory area per wolf (km²)	Finite rate of increase	Reference
			$\bar{x}$	N				
Moose	Isle Royale, Michigan	15,350	151	18	3.1	49	0.93	Peterson et al. 1998; R. O. Peterson, personal communication (1987–1991)
Moose	Isle Royale, Michigan	8,940	109	30	4.7	23	0.85	Peterson and Page 1988 (1980–1985)
Moose	Isle Royale, Michigan	7,920	181	24	7.4	24	1.04	Mech 1966b; Jordan et al. 1967; R. O. Peterson, personal communication (1959–1966)
Northeastern Minnesota, all years								
Deer	Northeastern Minnesota	4,572	198	198	5.8	34	0.99	Mech 1973, 1986; Mech and Nelson 2000; Peek et al. 1976; Fuller 1989b (1967–1985)
Northeastern Minnesota by wolf/deer trends								
Deer	Northeastern Minnesota	6,980	172	48	6.5	26	1.00	Mech 1986 (1967–1970)
Deer	Northeastern Minnesota	5,220	184	56	6.2	30	0.87	Mech 1986 (1971–1975); Mech and Nelson 2000
Deer	Northeastern Minnesota	3,900	219	94	5.2	42	1.00	Mech 1986 (1976–1985); Mech and Nelson 2000

Summary and statistical test results

Test[b]	r^2	d.f.	P	Regression
Biomass Index (BMI) and territory size	.33	31	$< .001$	$y = 900 - 0.07x$
BMI and pack size	.04	31	.29	
BMI and wolf density	.35	31	$< .001$	$y = 124 - 0.01x$
BMI and rate of increase	.008	21	.7	
Rate of increase and wolf density	.33	21	.005	$y = -104 + 181x$
Rate of increase and mean territory size	.30	21	.008	$y = -891 + 1407x$

Mean territory size and wolf density

Prey species	Deer	Moose
No. studies	11	13
Mean territory size	199	817
Mean wolf density	36	113

2-sample, two-tailed t-tests assuming equal variance

Test	d.f.	P	t
Mean territory size (deer v moose)	22	$< .001$	3.87
Mean wolf density (deer v moose)	22	$< .001$	3.89

Source: Adapted from Fuller 1989b.

[a]Relative biomass values were assigned as follows (similar to Keith 1983): bison, 8; moose, 6; elk, 3; caribou, 2; bighorn sheep, 1; Dall sheep, 1; mountain goat, 1; mule deer, 1; white-tailed deer, 1.

[b]Isle Royale and northeastern Minnesota data entered by phase of population trend. Other variations yielded similar results.

This variation may be related to prey type. Irrespective of ungulate biomass, all but two of twenty-four average wolf pack territory sizes, and two values for territory area per wolf, are higher ($P = .001$, two-tailed t test, d.f. = 22 for both territory size and area/wolf) where wolves prey mainly on moose than where they prey primarily on deer (see table 6.3). In areas of similar prey biomass, this relationship probably reflects the amount of prey biomass "accessible" to wolves. If moose are, on average, less vulnerable to wolf predation (i.e., harder to catch) than are deer, then we would expect a wolf pack of a particular size living on moose to need relatively more living biomass, and thus a larger territory, in order to provide enough prey that it can catch and kill.

There still remains much unexplained variation in territory size. Even in areas with the same major prey species and a similar total prey biomass, wolf pack territory sizes can differ markedly. For example, in southwestern Quebec boreal forest, moose ($230-370/1,000$ km^2 or $590-950/1,000$ mi^2) compose 100% of total ungulate prey biomass (see table 6.2), and wolf territories average $250-400$ km^2 ($98-156$ mi^2). In the Yukon, moose ($62-353/1,000$ km^2 or $160-900/1,000$ mi^2) compose 75% of total ungulate prey biomass, generally inhabiting forest patches and tundra, and wolf pack territories average 1,300 to 1,500 km^2 ($508-586$ mi^2). Perhaps moose in particular, and ungulate prey in general, are less "vulnerable" when co-occurring with several other species in open habitats.

Reproduction

Age

Although there are recorded instances of captive wolves breeding at age $9-10$ months (Medjo and Mech 1976), the earliest that breeding in wild wolves has been documented is 2 years (Rausch 1967; Peterson, Woolington, and Bailey 1984; Fuller 1989b), except for some equivocal evidence of first-year breeding in the restored Yellowstone population (D. W. Smith, personal communication). In some areas, females do not usually breed until age 4 (Mech and Seal 1987; Mech et al. 1998). As with other species, age of first breeding in wolves probably depends on environmental conditions such as food supply. In addition, because wolves must find a vacant territory before rearing young, those in saturated populations may have to wait longer.

This considerable flexibility in age of first breeding could have important effects on population change.

Thus, when food is abundant, such as during severe winters that make prey more vulnerable to wolves or in low-density reintroduced or heavily controlled wolf populations, wolves could rear pups when younger, quickly making use of the newly available resources to increase their numbers.

Few wolves live longer than 4 or 5 years, but female wolves as old as 11 years have been known to produce pups in the wild (Mech 1988c). There is no evidence that females reach reproductive senescence before they die, as coyotes do (Crabtree 1988). However, old females may be replaced as breeders by their daughters (Mech and Hertel 1983) and, if they remain in the pack, become postreproductive (Mech 1995d) (see also Kreeger, chap. 7 in this volume).

Breeding Frequency

Female wolves are capable of producing pups every year, and in most areas except the High Arctic (Mech 1995d), packs usually produce pups each year. Most wolf packs produce only a single litter per year (Harrington et al. 1982; Packard et al. 1983), although two litters from two females per pack have been reported (Murie 1944; Clark 1971; Haber 1977; Harrington et al. 1982; Van Ballenberghe 1983a; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987; Mech et al. 1998), and in Yellowstone National Park there were three litters in one reintroduced pack (D. W. Smith, personal communication). Except for these unusual packs, if there are more than two female wolves older than 2 years in a pack, usually some do not breed, or if they do breed, they may resorb their fetuses (Hillis and Mallory 1996a) or fail to rear the pups. Thus populations with larger packs contain a lower proportion of breeders (Peterson, Woolington, and Bailey 1984; Ballard et al. 1987). Increased human harvest of wolves may result in smaller packs and territories and in the establishment of new packs in vacated areas, so that breeders then compose a higher proportion of the population and the rate of pup production increases (Peterson, Woolington, and Bailey 1984).

There is not yet a good explanation as to why packs in some areas more frequently include two females that produce pups (e.g., the East Fork pack in Denali National Park, Alaska) (Murie 1944; Haber 1977; Mech et al. 1998). Two founding packs in Yellowstone National Park have produced multiple litters in several consecutive years (D. W. Smith, unpublished data). Because these packs have a maximal food supply, this observation

suggests that a surfeit of food fosters multiple breeding in a pack. Surplus food would certainly minimize competition and thus delay dispersal (Mech et al. 1998), so perhaps the founding breeding female would become more tolerant of her daughters breeding (see Mech and Boitani, chap. 1 in this volume).

Litter Size

Wolf litter sizes tend to average about five or six (Mech 1970; table 6.4) except in the High Arctic, where fewer pups are produced (Marquard-Petersen 1995; Mech 1995d). Litter size was small for an unexploited population in Ontario ($\bar{x} = 4.9$; Pimlott et al. 1969) but large for exploited populations in Alaska ($\bar{x} = 6.5$; Rausch 1967) and northeastern Minnesota ($\bar{x} = 6.4$; Stenlund 1955), leading Van Ballenberghe et al. (1975) and Keith (1983) to suggest that litter size may increase with ungulate biomass per wolf. More recent data strongly confirm this assertion (Boertje and Stephenson 1992), with litter sizes across studies increasing an average of 31% with a sixfold increase in ungulate biomass available per wolf ($r^2 = .38$, $P = .01$, d.f. $= 16$, table 6.4).

Survival

Age and Sex

Wolf pups in most areas survive well through summer (table 6.5), probably because of a temporary abundance of a greater variety of food (Mech et al. 1998). Where canine parvovirus is prevalent, however, summer pup survival can be quite low (Mech and Goyal 1995). Pup survival is directly related to prey biomass (table 6.5), for the greater the biomass, the greater the chance that more will be accessible. Summer pup survival was almost doubled (0.89 vs. 0.48) where per capita ungulate biomass was four times greater (table 6.5). In northeastern Minnesota, pup condition and survival decreased during a decline in the deer population (Van Ballenberghe and Mech 1975; Seal et al. 1975; Mech 1977b). The percentage of pups in the population or in packs (see table 6.4) was highest in newly protected (Fritts and Mech 1981) and heavily exploited populations (Ballard et al. 1987), and probably reflected both larger litters and higher pup survival where ungulates were abundant (Pimlott et al. 1969; Keith 1974, 1983; Harrington et al. 1983), as well as a higher percentage of the population being reproductive (see above).

Mean prey biomass/wolf ratios and mean percent-ages of pups in fall and winter populations are not clearly correlated (see table 6.4), in contrast to the findings of Keith (1983) and Boertje and Stephenson (1992). Prey biomass/wolf ratios and percentages of pups in packs are somewhat correlated, however (see table 6.4); the percentage of pups in packs on the Kenai Peninsula increased from 26% to 46% when wolf harvest was high and available biomass per wolf increased (Peterson, Woolington, and Bailey 1984). Autumn can be a critical period as pup food requirements are maximized (Mech 1970), but prey supply and vulnerability diminishes. Thus, where food is insufficient, it is usually fall, rather than summer, when pups starve (Van Ballenberghe and Mech 1975).

During winter, pup survival may differ from that of yearlings and adults in the same area. Sometimes it is higher (Ballard et al. 1987; Potvin 1988; Gogan et al. 2000); at other times, it is lower (Mech 1977b; Peterson, Woolington, and Bailey 1984; Fuller 1989b; Hayes et al. 1991). Overall, documented yearling and adult wolf annual survival rates where humans have not purposely tried to eliminate a high proportion of wolves (e.g., Bjorge and Gunson 1983; Gasaway et al. 1983) vary from about 0.55 to 0.85 (table 6.6). There is no evidence that female wolf survival differs from that of males.

Residency Status

In some studies, dispersing wolves seem to have had lower survival than wolves of the same age that remained in packs (Peterson, Woolington, and Bailey 1984; Messier 1985b; Pletscher et al. 1997). Dispersing wolves travel through new areas, where they are not familiar with the distribution of prey, and must work harder to maintain their condition. They also are less familiar with the distribution of other wolves that may kill them, and they may be more likely to be struck by a vehicle or to meet humans that may kill them (see below). Elsewhere, mortality did not differ by residency status (Fuller 1989b; Ballard et al. 1997; Boyd and Pletscher 1999), and in a population disrupted by control mortality, dispersing wolves survived better than residents (Hayes et al. 1991).

Mortality

Natural Factors

Wolves die of a variety of natural causes, including starvation, accidents, disease, and intraspecific strife (table 6.7). On Isle Royale, where no human-caused deaths occur,

TABLE 6.4. Ungulate biomass/wolf ratio, litter size, and percentage of pups in wolf populations during late fall to early winter for several areas of North America

Location	Ungulate biomass per wolf[a]	Litter size[b] $\bar{x}$	N litters	Percentage of pups in packs	Number of pups per pack $\bar{x}$	N packs	Reference
Central Alaska	101[c]	4.6	7	—	—	—	Boertje and Stephenson 1992 (low prey density)
North-central Minnesota	161	6.1	5	46	3.2	36	Fuller 1989b
Northeastern Minnesota	164	—	—	49	2.6	24	Harrington et al. 1983 (Superior National Forest)
Interior Alaska	173	4.4	12	29	—	—	Gasaway et al. 1983
Algonquin Park, Ontario	175	4.9	10	32	1.9	—	Pimlott et al. 1969
Northeastern Alberta	186	4.8[d]	5	40[d]	—	—	Fuller and Keith 1980a
Southern Yukon	207	4.4	18	34	2.1	—	Hayes et al. 1991
Southern Quebec	236	5.6	10	—	—	—	Potvin 1988
Northeastern Minnesota	236	—	—	43	3.4	5	Van Ballenberghe et al. 1975
Isle Royale, Michigan	243	—	—	45	2.4	9	Peterson and Page 1988 (1984–1986)
Northeastern Minnesota	252	6.4	8	—	—	—	Stenlund 1955
Denali Park, Alaska	255	4.2[d]	23	43	3.8	91	Meier et al. 1995; Mech et al. 1998
Northwestern Alaska	267	5.3	22	—	—	—	Ballard et al. 1997
Central Alaska	285[c]	5.7	12	—	—	—	Boertje and Stephenson 1992 (medium prey density)
Northwestern Alberta	306	6.2	5	29	—	—	Bjorge and Gunson 1989
Denali Park, Alaska	334	—	—	39	5.4	5	Haber 1977
Kenai Peninsula, Alaska	345	5.0	5	36	3.8	15	Peterson, Woolington, and Bailey 1984
Jasper Park, Alberta	364	—	—	45	5.2	5	Carbyn 1974
Northwestern Minnesota	400	5.6[e]	8	44	2.7	21	Fritts and Mech 1981; Harrington et al. 1983
East-central Yukon	435	5.7	19	—	4.3	—	Hayes and Harestad 2000a,b
North-central Minnesota	617	—	—	45	3.3	3	Berg and Kuehn 1980, 1982
South-central Alaska	659	6.1	16	67	5.4	28	Ballard et al. 1987
Central Alaska	675[e]	6.9	15	—	—	—	Boertje and Stephenson 1992 (high prey density)

Summary and statistical test results

Test	r^2	d.f.	P	Regression
BMI/wolf and litter size	.38	16	.008	$y = 4.5 + 0.003x$
BMI/wolf and % pups in packs in fall	.32	15	.02	$y = 31 + 0.03x$
BMI/wolf and no. pups in packs in fall	.32	13	.04	$y = 2.15 + 0.004x$

Fetal litter sizes

Mean	5.5
N	164
No. studies	14

Source: Adapted from Fuller 1989b.

[a] From table 6.2, unless noted otherwise.

[b] Litter sizes are based on fetal observations unless noted otherwise.

[c] Average ungulate biomass estimate from Boertje and Stephenson 1992.

[d] Based on May–June observations.

[e] Based on May and July observations.

TABLE 6.5.   Summer wolf pup survival and ungulate biomass in various areas of North America

Location	Summer pup survival rate[a]	Ungulate biomass per wolf[b]	Annual finite rate of increase	Annual adult survival rate	Reference
Northern Wisconsin	0.39[c]	400[d]	1.16	0.82	Wydeven et al. 1995
North-central Minnesota	0.48	161	1.02	0.64	Fuller 1989b
Southern Yukon	0.48	207[e]	0.97	0.56[e]	Hayes et al. 1991
Northwestern Minnesota	0.57[f]	378[d]	1.13	0.72[d,g]	Fritts and Mech 1981
Northeastern Alberta	0.69[f]	231	1.21	0.86[g]	Fuller and Keith 1980a (AOSERP area)
East-central Yukon	0.75[c]	435[h]	1.49	0.84[g]	Hayes and Harestad 2000a,b
Kenai Peninsula, Alaska	0.76	345	1.03	0.67[g]	Peterson, Woolington, and Bailey 1984
South-central Alaska	0.89	659[e]	0.88	0.59[e,i]	Ballard et al. 1987
Denali Park, Alaska	0.91[j]	334	1.06/1.20[k]	0.73	Mech et al. 1998

Summary and statistical test results

Test	r^2	d.f.	P	Regression
BMI/wolf and rate of increase	.003	8	.9	
BMI/wolf and adult survival rate	<.001	8	.94	
BMI/wolf and summer pup survival	.26	8	.16	
BMI/wolf and summer pup survival[l]	.69	6	.02	$y = 0.40 + 0.0008x$

"Summer" pup survival summary statistics

Mean	0.66
SE	0.06
SD	0.19
Range	0.39–0.91
No. studies	9

[a]Calculated from average litter size (fetal unless noted otherwise) and average number of pups in fall, from table 6.4.

[b]From table 6.2.   [f]Based on summer, not fetal, litter size.

[c]Survival to or through winter.   [g]Survival rate for all ages combined.

[d]Wolf population expanding.   [h]Wolf population recovering from heavy exploitation.

[e]Wolf population heavily exploited.   [i]Excludes mortality due to control program.

[j]Pup survival from May observations (not fetal) to average number of pups in August.

[k]Rate of increase based on late winter and early winter population estimates respectively.

[l]Omits Mech et al. 1998 and Wydeven et al. 1995.

annual mortality due to starvation and intraspecific strife (mostly related to relatively low food availability) ranged from 0 to 57% and averaged 23.5% (± 3.3 SE) from 1971 to 1995 (Peterson et al. 1998). In the Superior National Forest from 1968 to 1976, annual wolf mortality rates ran from 7% to 65%, and 58% of that mortality was natural, primarily due to fall pup starvation and intraspecific strife (Mech 1977b). In Denali National Park, Alaska, annual mortality averaged 27% and varied from 13% to 41% from 1986 through 1994; most (81%) of the

mortality was natural (Mech et al. 1998). Elsewhere, average annual natural mortality has varied from 0% to 24% (average 11% ± 2% SE) in populations also subject to 4–68% human-caused mortality (see table 6.8 and below).

Diseases such as rabies, canine distemper, and parvovirus and parasites such as heartworm and sarcoptic mange might be important causes of death for wolves, but documentation is somewhat lacking (see Kreeger, chap. 7 in this volume).

TABLE 6.6. Age-specific dispersal rates of wolves and annual survival rates of nonresident wolves

Location	Dispersal rate			$\bar{x}$	Pack size	Survival rate		Ungulate biomass per wolf[a]	Finite rate of increase	References
	Adult	Yearling	Pup			Resident	Non-resident			
Northeastern Minnesota	3	83	35	—	—			145	1.04	Gese and Mech 1991 (1985–1989); Mech and Nelson 2000
Southern Quebec	—	—	—	—	5.7	(0.65)[b]		159	1.06	Messier 1985a,b (high prey area)
North-central Minnesota	17	49	10	35	6.7	0.67	0.52	161	1.02	Fuller 1989b
Northeastern Minnesota	7	70	19	—	6.4	(0.58)[b,c]		168	0.91	Gese and Mech 1991; Mech 1977a, 1986; Mech and Nelson 2000 (1969–1975)
Northeastern Minnesota	5	47	4	—	5.2			171	1.02	Gese and Mech 1991; Mech 1986; Mech and Nelson 2000 (1975–1985)
Southern Quebec	9[d]	76[d]	13[d]	—	5.6	(0.64)[b]		236	—	Potvin 1988
Northwestern Alaska	17	15	—	18	8.6	(0.55)[b,e]		267	0.88	Ballard et al. 1997
Kenai Peninsula, Alaska	(19)[f]		—	22	11.2	<10	0.38	345	1.03	Peterson, Woolington, and Bailey 1984
Northern Wisconsin	9	23	13		3.5	(0.82)[b,g]		400	1.16	Wydeven et al. 1995 (1986–1991)
Non-age-specific dispersal:										
Northwestern Alaska				13	8.4	(0.60)[b]		236	1.22	Ballard et al. 1997 (1987–1989)
Voyageurs Park, Minnesota				37	5.5	(0.75)[b]		277	—	Gogan et al. 2000
Denali Park, Alaska				28	6.9	(0.73)[b]		320	1.06/1.20[b]	Mech et al. 1998
East-central Yukon				25	6.8	(0.84)[b]		426	1.49	Hayes and Harestad 2000a,b

Summary and statistical test results

Test	r^2	d.f.	P	Regression
BMI/wolf and adult dispersal	.05	6	.64	
BMI/wolf and yearling dispersal	.44	6	.10	$y = 94 - 0.19x$
BMI/wolf and pup dispersal	.06	5	.65	

[a] From table 6.2, unless noted otherwise.

[b] Combined survival rate for all wolves > 6 months old.

[c] Apparent survival rate from Mech (1977a).

[d] Calculated from number of age-specific dispersals per month monitored (Potvin 1988, fig. 4).

[e] Includes period with rabies epidemic.

[f] Combined yearling and adult dispersal rate.

[g] Wolf population expanding.

TABLE 6.7. Known causes of deaths of wolves

Cause	Reference[a]
Accident	
Avalanche	Mech 1991b; Boyd et al. 1992
Starvation	Mech 1977a
Cliff fall	Child et al. 1978
Human (accidental)	
Train	L. D. Mech, personal observation
Vehicles	de Vos 1949
Human (purposeful)	
Aerial hunting	Stenlund 1955
Corrals	Young and Goldman 1944
Deadfalls	Young and Goldman 1944
Den digging	Young and Goldman 1944
Dogs	Young and Goldman 1944
Eagles (falconry)	Kumar 1993
Edge traps	Young and Goldman 1944
Fish hooks	Young and Goldman 1944
Guns	Young and Goldman 1944
Ice box trap	Young and Goldman 1944
Lassoing and hamstringing	Young and Goldman 1944
Piercers	Young and Goldman 1944
Pitfalls	Young and Goldman 1944
Poison	Young and Goldman 1944
Ring hunts and drives	Young and Goldman 1944
Salmon poisoning	Young and Goldman 1944
Set guns	Young and Goldman 1944
Snares	Young and Goldman 1944
Spears	Young and Goldman 1944
Steel traps	Young and Goldman 1944
Wolf knife	Young and Goldman 1944
Wildlife	
Bear, black	Joslin 1966
Bear, brown	Ballard 1980; 1982
Deer	Frijlink 1977; Nelson and Mech 1985
Moose	MacFarlane 1905; Stanwell-Fletcher and Stanwell Fletcher 1942
Muskox	Pasitchniak-Arts et al. 1988
Wolves	Murie 1944; Mech 1994a
Disease	
Canine parvovirus	Mech et al. 1997
Distemper	Grinnell 1904
Encephalitis	Young and Goldman 1944
Mange	Young and Goldman 1944
Rabies	Young and Goldman 1944; Chapman 1978

[a]First (and other significant) reference(s) in the scientific literature.

Human-Related Factors

Over the years, humans have devised many ways to kill wolves (see table 6.7). With focused wolf reduction programs, populations have been reduced over 60% in some years (table 6.8). In a few cases, site-specific control programs have eliminated entire packs (Fritts et al. 1992; Hayes et al. 1991; T. K. Fuller, unpublished data). Since wolves were legally protected in Minnesota and Wisconsin in 1974, human-caused wolf deaths have taken 13–31% of the studied populations there annually (Mech 1977b; Fritts and Mech 1981; Berg and Kuehn 1982; Fuller 1989b; Gogan et al. 2000). In Wisconsin, human-caused mortality declined after 1986, from 28% to 4%/year on average (Wydeven et al. 1995).

Many of the human-caused deaths in protected wolf populations occur because of depredations on livestock (see Fritts et al., chap. 12 in this volume). The government control program in Minnesota, for example, accounted for the deaths of 161 wolves there in 1998 (Mech 1998b), or about 7% of the population. Private citizens also kill wolves illegally to protect livestock, pets, and even deer (Fritts and Mech 1981; Berg and Kuehn 1982; Fuller 1989b; Corsi et al. 1999), or for other reasons. Wolves also are killed accidentally when hit by cars or trains, and are captured in traps or snares set for other wildlife species. Some are mistakenly shot as coyotes, but historically this source of mortality has been lower than intentional killing (Berg and Kuehn 1982; Fuller 1989b).

In examining factors correlated with the historic demise of wolves in Wisconsin, Thiel (1985) found that, in the era when wolves were persecuted by people, wolf populations did not survive where road densities exceeded about 1 km/km², because the roads made these areas accessible to people who killed wolves illegally or accidentally. Other studies supported that conclusion (Jensen et al. 1986; Mech, Fritts, Radde, and Paul 1988; Fuller 1989b). However, after public attitudes toward wolves changed (Kellert 1991, 1999) and wolves greatly increased and expanded their range, wolf populations have been able to survive even where road densities are higher than 1 km/km² (Mech 1989; Fuller et al. 1992; Berg and Benson 1999). Wolves are successfully occupying areas where road and human densities were thought to have been too high 10 years ago (Berg and Benson 1999; Merrill 2000).

Dispersal

Dispersal is a major means by which maturing wolves of both sexes leave their natal packs, reproduce, and expand their population's geographic range. Dispersers also fill any gaps in a population's territorial mosaic left by packs that have died or been killed out (see Mech and Boitani, chap. 1 in this volume). They also serve as sources for "sink" populations that could not sustain themselves without immigration from elsewhere (Mech 1989; Lariviere et al. 2000). Most often, dispersing wolves establish territories or join packs located anywhere from near their natal pack to some 50–100 km (30–60 mi) away (Fritts and Mech 1981; Fuller 1989b; Gese and Mech 1991; Wydeven et al. 1995). However, they sometimes move much longer distances; one disperser traveled at least 886 km (532 mi) away from its home area (Fritts 1983).

Several factors affect the timing and age of dispersal (Mech et al. 1998). Whether wolves pair and settle in a vacant area (Rothman and Mech 1979; Fritts and Mech 1981; Ballard et al. 1987) or join already established packs (Fritts and Mech 1981; Van Ballenberghe 1983b; Peterson, Woolington, and Bailey 1984; Messier 1985a; Mech 1987a) probably depends on relative prey abundance, the availability of vacant territories, and survival rates of breeding pack wolves.

Across populations, annual dispersal rates range from 10% to 40%, with most variation due to the irregular dispersal of nonbreeding wolves older than 1 year (see table 6.6). When food is sufficient, few yearlings may be driven to disperse ($r^2 = .44, P = .10$, d.f. $= 7$), although in unsaturated populations nonbreeding wolves may leave at younger ages to take advantage of breeding opportunities (Fritts and Mech 1981). Thus dispersal age is what varies most. Most adult dispersal (see table 6.6) consists of nonbreeding wolves 2 years old or older; these animals disperse at rates similar to those of yearlings (once breeding wolves are removed from the analysis).

Rates of Population Change

Potential

L. D. Mech once saw a vacant wolf territory in the Superior National Forest colonized by a new pair of radio-collared wolves one summer, and a year later the pair had produced seven pups. Wolves in that territory thus increased from two to nine, or 450%, in one year. Small

TABLE 6.8. Mean rates of population increase and annual mortality rates of exploited wolf populations in North America

Location	Number of years	Population increases		Annual mortality rate		Reference
		Finite rate	Exponential rate	Total	Human-caused	
Northwestern Alberta	2	0.40	−0.92	0.68[a]	0.68	Bjorge and Gunson 1983
Interior Alaska	4	0.76	−0.27	0.58	0.50	Gasaway et al. 1983; Ballard et al. 1997
Southwestern Manitoba	4	0.86	−0.15	0.56	0.32	Carbyn 1980
South-central Alaska	8	0.88	−0.13	0.45	0.36	Ballard et al. 1987
Northwestern Alaska	5	0.88	−0.13	0.45	0.27	Ballard et al. 1997
Northeastern Minnesota	6	0.89	−0.12	0.42	0.18	Mech 1977a, 1986 (1970–1976)
North-central Minnesota	3	0.93	−0.08	0.31	0.31	Berg and Kuehn 1982
Southern Yukon	6	0.97	−0.03	0.60	0.40	Hayes et al. 1991
Isle Royale, Michigan	4	0.95	−0.05	0.34	0.00	Peterson and Page 1988 (1983–1986)
Isle Royale, Michigan	9	1.01	0.01	0.21	0.00	Peterson et al. 1998
Algonquin Park, Ontario	5	1.01	0.01	0.37	0.24	Forbes and Theberge 1995
North-central Minnesota	6	1.02	0.02	0.36	0.29	Fuller 1989b
Kenai Peninsula, Alaska	6	1.03	0.03	0.33	0.28	Peterson, Woolington, and Bailey 1984
Denali Park, Alaska	8/9[b]	1.06/1.20	0.06/0.18	0.27	0.05	Mech et al. 1998
Southwestern Quebec	4	1.06	0.06	0.35	0.30	Messier 1985a,b (high prey area)
Northwestern Minnesota	5	1.13	0.12	0.28	0.17	Fritts and Mech 1981
Northern Wisconsin	6	1.16	0.15	0.18	0.04	Wydeven et al. 1995 (1986–1992)
Northeastern Alberta	3	1.21	0.19	0.15	0.15	Fuller and Keith 1980a (AOSERP area)
East-central Yukon	6	1.49	0.40	0.16	0.02	Hayes and Harestad 2000a,b

Summary and statistical test results

Test	r^2	d.f.	P	Regression
Total mortality and rate of increase	.7	18	< .001	$y = 1.4 - 1.17x$
Human-caused mortality and rate of increase	.6	18	< .001	$y = 1.2 - 0.93x$
BMI/wolf[c] and rate increase	.004	18	.80	
BMI/wolf and total of mortality	.07	18	.29	
BMI/wolf and human-caused mortality	.03	18	.46	
Human-caused mortality and wolf density	.04	18	.43	
Total mortality and wolf density	.003	18	.83	
Human and total mortality	.72	18	< .001	$y = 0.2 + 0.73x$
Human and natural mortality (no Isle Royale)	.14	16	.15	

Mortality summary statistics	Total	Human	Natural
Mean	0.37	0.24	0.11
SE	0.04	0.04	0.02
SD	0.15	0.18	0.08
Range	0.15–0.68	0–0.68	0–0.24
No. studies	19	19	17

[a] Mortality rate of early winter population; assumes all mortality is human-caused and summer survival of adults = 1.00.

[b] For spring and fall estimates, respectively. [c] Biomass Index from table 6.2 and Peterson et al. 1998; Mech 1977a; 1986.
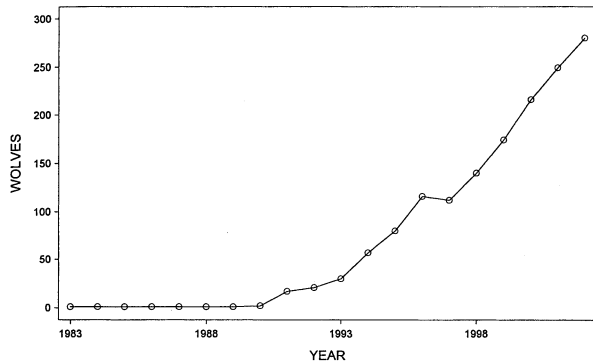
FIGURE 6.3. Trend of a colonizing wolf population in Michigan. Wolves spread from Minnesota into Wisconsin and by 1990 from Wisconsin into Michigan. A small proportion of Michigan wolves may also have immigrated from Ontario. This population trend represents an expanding population, not a density change. (From Michigan Department of Natural Resources 1997 and unpublished data.)

wolf populations have increased as much as 90% (from 30 to 57) from one year to the next (Michigan Department of Natural Resources 1997).

Populations that increase at such high rates are usually those that (1) have recently colonized or recolonized new areas (e.g., in Wisconsin, Michigan, and Yellowstone National Park), (2) have rebounded after deliberate removal of a subpopulation from within a much larger population (Ballard et al. 1987; Boertje et al. 1996; Hayes and Harestad 2000a), as Keith (1983) postulated, or (3) have been heavily harvested (see table 6.8) or devastated by disease (Ballard et al. 1997).

The population of wolves recolonizing the Upper Peninsula of Michigan increased by 90% in 1993 and at a mean rate of about 58%/year from 1993 through 1996 (fig. 6.3) (Michigan Department of Natural Resources 1997). In Bieszczady National Park, Poland, where wolves were heavily harvested, annual increase ranged from 15% to 53% (Smietana and Wajda 1997). The recolonizing Scandinavian wolf population increased an average of 29% from 1991 through 1998 (Wabakken et al. 2001). Given such high potential rates of increase and adequate food, wolf populations can more than double in 2 years.

Reproduction

The main component of dramatic increases in wolf numbers is reproduction, especially pup survival to fall. Because the single largest age class of wolves in a pack and in a population is the young-of-the-year, it is easy to

see that annual change in pack or population size is most dependent on the fate of pups. In north-central Minnesota, annual wolf population change was highly correlated ($r^2 = .79$; $P < .02$) with the average number of pups per pack the previous fall (Fuller 1989b). Similarly, in Denali National Park, Alaska, from 1986 through 1993, 80% of the annual variation in spring-to-spring percent wolf population change was attributable to percent pup production and survival to the previous fall (Mech et al. 1998). In the Superior National Forest, percent change in the winter wolf population was correlated ($r^2 = .39$; $P = .05$) with an index of pup production in the previous summer (Mech and Goyal 1995).

It is interesting that in the unexploited wolf population on Isle Royale, where neither immigration nor emigration is a factor, the relationship between pup percentage (combined reproduction and pup survival to winter) and population change was only 35% (Peterson et al. 1998). Probably mortality influenced the dynamics of this isolated population more than did reproductive success because mortality rates varied more among years (Peterson et al. 1998).

Immigration

Depending on the reproductive status of wolf populations in surrounding areas, immigration could also provide a major component of population increase in areas where the potential for wolf density is relatively high. Especially in areas where intensive wolf control has been conducted, dispersal from adjacent populations can quickly resupply breeding pairs, which then produce large litters, recolonize the control zone, and within 2–4 years refill the area where wolves had been almost eliminated (Gasaway et al. 1983; Ballard et al. 1987; Potvin et al. 1992; Hayes and Harestad 2000a).

Mortality

For a wolf population, like any other wild population, mortality is a year-round process. Theoretically, as soon as wolf pups are born, mortality can begin, and no doubt this sometimes occurs. Because newborn pups remain in the den for their first 10–24 days (Young 1944; Clark 1971; Ryon 1977; Ballard et al. 1987), however, it is almost impossible to measure early pup mortality.

Most often the best that can be done, without disturbing the pups and the adults by invading the den—and thus possibly affecting the study results—is to count the

pups when they first emerge from the den. By then, of course, some might already have died. Even regularly observing pups around a den is difficult or impossible in many areas. Thus data on wolf pup mortality often are based on a comparison of pup numbers around a den or rendezvous site in summer versus fall, when they can be seen and distinguished from the air (Fritts and Mech 1981; Fuller and Keith 1980a; Mech et al. 1998). Some pups can be identified from the air even in winter, but workers disagree on how consistently that can be done (cf. Van Ballenberghe and Mech 1975 and Peterson and Page 1988). An alternative approach is comparing fetal litter sizes (from carcasses) with average fall litter sizes in the same area (Peterson, Woolington, and Bailey 1984; Hayes et al. 1991).

Causes and rates of pup mortality were discussed above. However, we wish to emphasize here that most reported wolf mortality rates (see table 6.8) pertain to the population of wolves aged about 4–8 months and older. Mortality rates for younger pups usually remain unknown for two reasons: first, wolf pups are usually not large enough to be caught and radio-collared until they are at least 4–6 months old (Van Ballenberghe and Mech 1975), and second, many mortality studies depend on aerial observation of wolves, which is usually not feasible until winter. Reported annual mortality rates, then, are likely to be lower than if pups younger than 6 months old were included because pup mortality generally exceeds that of older wolves during late spring and summer.

Because of their high reproductive potential, wolf populations can withstand a high rate of mortality. On Isle Royale, where pups constitute a smaller percentage of the population than usual and wolves do not disperse to and from the island, annual natural mortality of adult-sized wolves averaged 15% when numbers were increasing or stable, 41% during population declines, and 24% when the population was stable (Peterson et al. 1998). Of course, in most populations, in which litters average five or six pups (Mech 1970), sustainable mortality can be even higher because this mortality keeps a higher percentage of the population breeding (Peterson, Woolington, and Bailey 1984) (see above).

If exploitation rates are too high to be fully compensated for by reproduction, however, the population should decline. Observed rates of increase are, as expected, negatively correlated with both total mortality ($r^2 = .70$; $P < .001$, d.f. = 19) and human-caused mor-

tality ($r^2 = .60$; $P = < .001$, d.f. = 19) (see table 6.8). These relationships suggest that, on average, wolf population size should stabilize ($r = .00$, $\lambda = 1.00$) with a mortality rate of 0.34 ± 0.06 SE, or a human-caused rate of 0.22 ± 0.08 SE, in late autumn populations of wolves (i.e., excluding mortality from birth to autumn). The slope of this relationship between intrinsic rate of increase and mortality, however, is fairly gentle. Thus even a considerable amount of additional mortality does not necessarily reduce the population so much that it cannot compensate or rebound through increased reproduction and/or immigration (Lariviere et al. 2000).

As recovering wolf populations continue to grow (see Boitani, chap. 13 in this volume), managers and the public will become increasingly interested in both sustainable levels of wolf harvest and the percentage take necessary to reduce a population or keep it stable (Mech 2001a). Because the above figures represent a general average, it is also useful to examine the results of specific studies dealing with the subject in order to better understand the high degree of variation that is possible.

Mortality Rates for Control and Sustainable Harvest
The maximum percentage of a wolf population that can be harvested annually on a sustainable basis is just short of the percentage that must be taken to control a wolf population. Thus we will discuss these two figures as one. By "control" we mean keeping a wolf population below the level to which it would rise without human-caused mortality.

Mech (1970, 63–64) suggested that over 50% of the wolves over 5–10 months old must be killed each year to control a wolf population, basing his estimate on Rausch's (1967) age structure data on over 4,000 harvested Alaskan wolves. Because these wolves were killed in fall and winter, the 50% kill figure would have been in addition to natural mortality from birth to 5–10 months of age. Keith (1983) reevaluated the proposed 50% kill figure by assembling data from several field studies. He concluded that the figure should be less than 30%, including a precautionary hedge. However, the data he used (Keith 1983, table 8) included populations that may have been stationary when 41% were taken, and declining populations with a 58–70% take. These data do not conflict with the 50% figure.

Other studies have directly measured the effects of various harvest rates. Gasaway et al. (1983) reported stable wolf populations after early winter harvests of 16–24%,

but declines of 20–52% after harvests of 42–61%. On Alaska's Kenai Peninsula, wolf density dropped following two annual kills of over 40%, but increased 58% after a harvest of 32% (Peterson, Woolington, and Bailey 1984). Elsewhere in Alaska, Ballard et al. (1987) estimated that a 40% human take of the fall wolf population caused a decline. By reanalyzing their data, however, Fuller (1989b) concluded that the population would stabilize with a total overwinter mortality of 34%, including a fall harvest rate of 27%.

Fuller (1989b) also concluded that, in north-central Minnesota, a human-caused annual mortality rate of 29% resulted in a stable or slightly increasing wolf population. This finding is supported by similar work in Poland's Bieszczady National Park. There, annual mortality of 21–39% ($\bar{x} = 29\%$) of the 26–33 wolves in five packs, in a population with little or no immigration, resulted in a stable or slightly decreasing population (Smietana and Wajda 1997).

Additional evidence that human take of wolves can sometimes exceed 35% without permanently reducing a population comes from the annual rates of increase of the colonizing Michigan wolves discussed earlier. The figures imply that from 1993 to 1996, if humans had killed 58% of the wolves each year, the population would only have remained stable rather than continuing to increase.

These latter figures are much lower than one derived from a 5-year study in northwestern Alaska. There, wolf numbers remained stable at an annual winter mortality rate of 53%, including a minor amount of natural mortality (Ballard et al. 1997). The harvest in this study was biased toward nonreproductive animals, which may typify human-caused mortality; variation in this proportion probably helps explain the variation found among studies (Fuller 1989b).

The highest mean annual sustained human take of wolves was 74%, reported from the Portneuf Wildlife Reserve in Quebec, Canada, from 1990 to 1997 (Lariviere et al. 2000). The authors believed that the population there, and in nearby reserves, was being maintained by wolves immigrating from surrounding areas.

Causes of Variation in Sustainable Mortality Rate

Why all the variation in this important figure? Fuller (1989b, 25) noted that "these values may vary with the age and sex structure of the population. For example, a population with a high proportion of pups may be able to withstand somewhat higher overall mortality because pups (non-reproducers) may be more vulnerable to some harvest techniques and make up a disproportionate part of the harvest. Also, net immigration or emigration may mitigate effects of harvest." Ballard et al. (1997, 24) agreed, adding that "relatively small packs can sustain high mortality rates so long as reproductively active adults are not killed." These authors also stressed that multiple denning within individual packs (Harrington et al. 1982; Ballard et al. 1987; Mech et al. 1998) could significantly affect rates of increase and sustainable mortality rates.

Boiled down to its essence, the factor most critical to the annual percentage of a wolf population that can be killed by humans without reducing the population is the population's productivity. Clearly, if productivity is low, or immigration limited, then allowable harvest must be low as well, and field studies confirm that conclusion (Peterson, Woolington, and Bailey 1984; Fuller 1989b; Ballard et al. 1997). However, where productivity is average or high, a much higher take can be sustained, especially if the harvested or controlled population is surrounded by a population with a lower human take that can serve as a source population (Gasaway et al. 1983; Ballard et al. 1987; Hayes and Harestad 2000a,b; Lariviere et al. 2000).

Compensatory Mortality

As in other populations, the principle of compensation (Errington 1967) operates in wolf populations (Mech 2001a). This principle, simply stated, means that wolves killed by one factor cannot be killed by another. Thus, for example, if some wolves are killed by humans, there are fewer wolves that can starve or be killed by other wolves, the two main sources of natural wolf mortality (see above). Also, survival prospects may improve for the remaining wolves due to greater food availability or fewer conflicts, thus further reducing natural mortality. In addition, a population reduction can lead to increased reproduction through higher litter sizes and/ or higher pup survival (see above). However, human-caused mortality can compensate for natural mortality even if it does not affect the rate of natural mortality (R. G. Haight, personal communication).

In Minnesota, where wolves were legally protected from human hunting by the federal Endangered Species Act and illegal human-caused mortality was 17–31% (Mech 1977b; Fritts and Mech 1981; Berg and Kuehn

1982; Fuller 1989b), and in Denali National Park, Alaska, where wolves in much of the area are protected by the National Park Service, some 10% of the population each year was killed by other wolves (Mech 1977b; Mech et al. 1998). However, in parts of Alaska where wolves are legally hunted and trapped by humans at a rate of 28–38%, very few wolves are killed by other wolves (Peterson, Woolington, and Bailey 1984; Ballard et al. 1987, 1997). Another indication of how natural and human-caused mortality compensate for each other can be found in the relationship between rates of total mortality and human-caused mortality, where human take replaces about 70% of mortality that would have occurred otherwise ($r^2 = .72$, $P < .001$, d.f. = 19; see table 6.8).

Because of the compensatory nature of various mortality factors, if humans wish to control a wolf population (keep it stable or reduce it), they must kill a higher percentage of wolves than would be expected to die of natural causes in a stable or increasing population. In addition, control measures must be carried out for several consecutive years, or the population bounces back.

A good example can be seen in the Tanana Flats area south of Fairbanks, Alaska. During a 7-year period, a population of 239 wolves was reduced to about 143 animals, but 337 wolves had to be killed to effect that reduction (Boertje et al. 1996). A take of 61% of the population in the first year and 42–43% of the remaining number in each of the next 2 years reduced the population, but a take of 38% in the fourth year then affected it little. A 19% kill in the fifth year was followed by a 51% population increase. In a review of wolf control in Alaska and elsewhere, a U.S. National Academy of Sciences committee concluded that wolf control is likely to be successful only if, among other things, "wolves are reduced to at least 55% of the pre-control numbers for at least 4 years" (National Research Council 1997, 184).

No doubt some of the resistance of the Tanana Flats wolf population to reduction came from dispersing wolves from the surrounding area (Hayes and Harestad 2000a). However, in addition, much of the high human kill, especially in the first 2 years, merely compensated for any natural mortality that might have taken place and fostered an increase in the percentage of breeders, as detailed earlier.

The relationship between dispersal and compensatory mortality involves two main aspects. First, an important factor in wolf dispersal is food competition. The greater the food competition, the more likely maturing wolves are to disperse (see above and Mech and Boitani,

chap. 1 in this volume). Human-caused mortality, especially when heavy, reduces food competition, which in turn reduces dispersal. Thus wolves that might have been lost from the population through dispersal remain, helping to compensate for the human-caused mortality. This mechanism operates, of course, only if the dispersal from the population would have exceeded the dispersal into it from the surrounding area.

The second aspect of the dispersal-compensation relationship involves the flux of lone, nonresident wolves circulating through the population. These animals are searching for opportunities to take up breeding positions by inserting themselves and a mate among the existing pack territorial mosaic, by joining an existing pack, or by colonizing areas at the edge of the population's range (see Mech and Boitani, chap. 1 in this volume). If a wolf population is subjected to human control, that creates vacancies both in packs and in territories that these floaters can fill. Thus the controlled population becomes a sink for wolves immigrating from as far as hundreds of kilometers away. These wolves then help compensate for the wolves being killed.

Wolf Population Models

Wolf populations have been the subject of several attempts to understand and predict their trends by mathematically modeling their dynamics. Efforts have ranged from the simple correlating of wolf density and prey biomass to highly complex computerized models that include consideration of age-specific mortality rates, varying reproductive rates, immigration, dispersal, spatial organization, and various life history relationships.

The first wolf population model was Keith's (1983) correlation of wolf density with prey biomass, which Fuller (1989b) extended and Dale et al. (1995) refined. While it is valuable for describing general relationships, this correlation's wide confidence intervals limit its value in predicting wolf density or population trends at specific locations and times (Mech et al. 1998). Population viability analysis (PVA) models based on computerized demographic simulations (Soulé 1980, 1987; Seal and Lacy 1989) have also been applied to wolves (USFWS 1989; Ciucci and Boitani 1991; D. R. Parsons, personal communication, cited in Fritts and Carbyn 1995). However, for several reasons, they have proved unsatisfactory or even misleading (Caswell 1989; Boyce 1992; Fritts and Carbyn 1995; White 2000). Similarly, a stochastic population model to predict wolf numbers in Yellowstone Na-
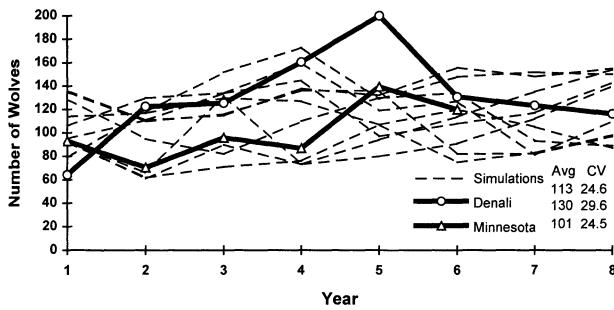
FIGURE 6.4. Annual variation in population sizes from ten random simulations of the Cochrane (2000) wolf population model compared with actual data from north-central Minnesota (Fuller 1989b) and Denali National Park, Alaska (Mech et al. 1998) for average fall/winter pack sizes extrapolated to equivalent fifteen-territory areas. The coefficient of variation for the model was based on thirty random simulations. (From Cochrane 2000.)

tional Park after reintroduction (Boyce 1990) proved problematic (see Boitani, chap. 13 in this volume), even though it incorporated prey dynamics.

More recent wolf population models have included consideration of wolf social structure, and one of them (Vucetich et al. 1997, 957) predicted that "demographic stochasticity may pose the greatest threat to small, isolated wolf populations," an interesting conclusion that has yet to be tested. Modern models include consideration not only of wolf social structure, but also of wolf population territorial structure (Haight and Mech 1997; Haight et al. 1998, 2002; Cochrane 2000). Obviously the greater the number of critical factors a model includes, the greater the chance that it will faithfully simulate reality. The Cochrane (2000) model, for example, tests well in generating wolf population trends similar to those actually described (fig. 6.4).

Natural Wolf Population Regulation

Although most wolf populations worldwide are strongly influenced by humans through control, harvesting, or illegal or incidental taking, valuable insight into wolf population dynamics can be gained by examining a few wolf populations under natural regulation. The key question to be asked about these populations is what is driving or regulating them.

Intrinsic Population Control

The idea that wolves might regulate their own numbers has been entertained by researchers as far back as Adolph Murie (1944, 15) who wrote that "intraspecific intolerance may hold a population in check." Stenlund (1955), Mech (1966b, 1970), Pimlott (1967, 1970), Woolpy (1967), and Van Ballenberghe et al. (1975) have added to the speculation. As indicated by Mech and Boitani in chapter 1 in this volume, wolf populations are characterized by various mechanisms that might contribute to intrinsic regulation of their numbers: territoriality, intraspecific strife, high dispersal rates, and reproductive inhibition in subordinate pack members and lone wolves. Mech (1970) discussed how these various intrinsic mechanisms might work, and Pimlott (1970) concluded that such mechanisms operate to regulate wolf numbers at about 40/1,000 km^2 (102/1,000 mi^2).

However, as more and more data accumulated, it became increasingly clear that, while social factors might play some role, it was available food that ultimately limited wolf populations. Mech (1970, 317) mentioned this possibility—"Of course, if there were no other factors controlling a wolf population, ultimately it would be limited by a shortage of food"—and stressed that "food" meant "vulnerable prey." Van Ballenberghe et al. (1975, 36) stated similarly that "environments rich in food lower the threshold of such [intrinsic] mechanisms and are the ultimate factor accounting for the existence of dense wolf populations." Packard and Mech (1980, 1983) viewed the intrinsic limitation theory as "outdated" and reiterated the importance of vulnerable prey biomass. Keith's (1983) synthesis nailed the coffin of the intrinsic regulation theory shut with his findings of the importance of per capita prey biomass to wolf population dynamics.

Vulnerable Prey Biomass

Thus, although the intrinsic social characteristics of wolves modulate the way in which wolf populations react to their vulnerable prey biomass (Packard and Mech 1980), ultimately wolf numbers depend on the food supply, except when limited by disease. The combination of reproduction, mortality, immigration, and dispersal determines wolf population levels at any given time (see above). Changes in numbers from year to year depend on how these factors are affected by food, and that can vary over time or space.

Although the general relationship between food supply (prey biomass) and wolf numbers is strong (Keith 1983; Fuller 1989b; see table 6.2), it is also highly variable. Thus, for a given prey biomass, wolf numbers can vary

as much as fourfold (Fuller 1989b). As indicated by Mech and Peterson in chapter 5 in this volume, not all prey animals are accessible to wolves. Rather, it is the older, weaker, younger, and otherwise vulnerable individuals in the prey population that wolves generally kill. Thus, although on average a large prey herd should contain more vulnerable members than a small one, it is possible for a large herd to include fewer vulnerable members than a small one, and vice versa. A large, increasing herd, for example, will be younger on average, and thus will include fewer vulnerable individuals, than a small, decreasing, and thus older, herd. Because prey condition is highly dependent on weather conditions (Mech and Peterson, chap. 5 in this volume), and weather is so variable, the annual percentage of a herd that is vulnerable is also highly variable.

Therefore, we agree that the proper unit of prey biomass to consider in analyzing wolf-prey interactions is vulnerable prey biomass. Although vulnerable prey biomass is an ever-changing proportion of a prey herd and is seldom measurable, the concept is critical to an understanding of wolf-prey relations and wolf population dynamics.

Fortunately, sometimes a single vulnerability factor is so overwhelmingly important that vulnerable prey biomass can be measured. For example, in one of the most elegant findings of any wolf-prey study done anywhere, the trend in numbers for the long-studied Isle Royale National Park wolf population (fig. 5.6) was found to depend on the number of moose (their sole year-round prey) 10 years old or older (Peterson et al. 1998). From 1959 to 1980 and from 1983 to 1994, the number of wolves was related to the number of old moose ($r^2 = .80$ and $.85$, respectively).

In Denali National Park, Alaska, where humans also have little effect on the wolf population, the trend in wolf numbers from 1986 through 1994 (fig. 6.5) was driven by snow depth, which influenced caribou vulnerability (Mech et al. 1998). Although Denali wolves fed primarily on moose, caribou, and Dall sheep, the vulnerability of caribou was the main determinant of wolf population change during the study. As snow depth and caribou vulnerability increased, adult female wolf weights also increased, followed by increased pup production and survival and decreased dispersal (Mech et al. 1998).

A more complicated situation existed in the east-central Superior National Forest of Minnesota (fig. 6.6). There wolves were protected by the Endangered Species
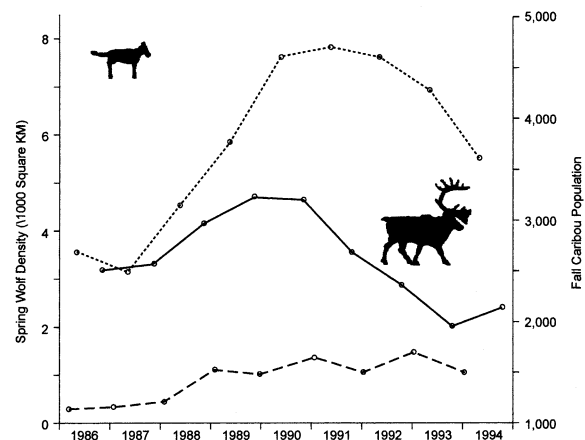

FIGURE 6.5. Wolf and caribou population trends in Denali National Park, Alaska, 1986–1994, in relation to snow-depth trend (bottom graph). Other important prey of these wolves are moose and Dall sheep, but wolf numbers changed in relation to caribou numbers. (From Mech et al. 1998.)
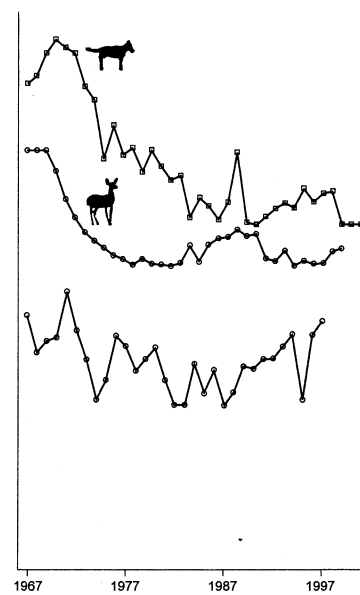

FIGURE 6.6. Wolf and white-tailed deer trends in the east-central Superior National Forest of Minnesota (Mech 1973, 1977b, 1986, 2000c) in relation to trend in cumulative 3-year snow depth (Mech et al. 1987 and unpublished). Deer population for 1967–1974 subjectively based; for 1975–1985 based on Nelson and Mech (1986a); and for 1986–1999 based on projections from correlation ($r = .31$; $P = .09$) between reported buck kill in Isabella area (M. Lennarz, personal communication) and winter deer counts in the same area (Nelson and Mech 1986a) for 1975–1976 through 1984–1985. Note that the wolf population trend followed the deer population trend through about 1984, when canine parvovirus affected the wolf population (Mech and Goyal 1995; L. D. Mech and S. M. Goyal, unpublished data).

Act of 1973 in August 1974. Although poaching by humans continued (Mech 1977b), it was not enough to reduce the population. From about 1966 to 1983, the wolf population trend (Mech 1973, 1977b, 1986) followed that of the white-tailed deer herd (cf. Mech 1986 and Nelson and Mech 1986a; Mech and Nelson 2000), which was related to winter snow depth (Mech and Frenzel 1971a; Mech and Karns 1977; Mech, McRoberts et al. 1987). Thus snow was seen as the driving force in the wolf-deer system (Mech 1990a). However, canine parvovirus (CPV), a new disease of domestic dogs that apparently began as a laboratory artifact, began to spread to the wolf population in the late 1970s, and by 1984 began influencing the wolf population (Mech and Goyal 1995), thereby at least partly unlinking wolf and deer numbers (Mech and Nelson 2000, fig. 2).

From the above three long-term investigations of wolf population trends, we can conclude that the factors that determine the annual changes in natural wolf populations are usually those affecting the availability of wolf prey. Prey availability is determined by prey density and vulnerability, so theoretically habitat quantity and quality, weather conditions, and competing predators (including humans) all can ultimately affect wolf numbers. The role of CPV in the Superior National Forest population can be considered an artifact. Wolves are well adapted to most diseases, and their populations are not usually affected by most of them (but cf. Carbyn 1982b), except perhaps by rabies (Chapman 1978) in the far north (see Kreeger, chap. 7 in this volume).

Cumulative Effects

Although there are no experimental studies per se on the accumulated effects of a variety of potentially negative factors on wolf populations (sensu Salwasser and Samson 1985; Weaver et al. 1987), none may be required. While it is difficult to test specific factors alone and in combination and then determine their joint effects on wolf demography (but see Cochrane 2000), the significant factors affecting wolf population trends are well studied (see above). The relative impact of concurrent effects can be deduced from the knowledge we currently have (e.g., relations between food abundance and productivity and survival, and human propensity to kill wolves). Simple demographic models (Keith 1983; Fuller 1989b) account for most observed differences in wolf population levels, and Cochrane's (2000) more compre-

hensive model allows more sophisticated exploration of the effects of multiple factors. Also, we know that wolves are very adaptable (i.e., can live under a great variety of circumstances) and can pass on adaptive behaviors to their offspring; few disturbances short of extensive killing affect wolf population demography.

Given the limits on our ability to assess the distribution, density, and mortality of wolves and their prey, our knowledge of the significant aspects of wolf biology is reasonably detailed and is unlikely to get much better. Even Geographic Information System-based landscape analyses (Mladenoff et al. 1995, 1999) of the Lake Superior Region, while confirming and refining earlier findings (Thiel 1985) about the relationship of wolf distribution to road densities and other landscape features, added little new information. Because of the overwhelming effort that has already gone into wolf studies, it seems unlikely that more complex landscape-explicit models (e.g., Weaver et al. 1987) will greatly improve our accuracy in predicting cumulative effects.

Persistence of Wolf Populations

Wolf populations possess a remarkable ability to persist so long as food supply is adequate, despite being subject to a number of possible mortality factors (see above). Even small populations of wolves have persisted and increased in several areas of the world during the last three decades. Because wolves were exterminated across almost all of the forty-eight contiguous United States, Mexico, and most of western Europe, many people think of the species as being fragile. However, it was primarily through poisoning that wolves were extirpated (Fritts et al., chap. 12, and Boitani, chap. 13 in this volume). Now that poison has been outlawed or greatly restricted in many areas, wolf populations are rebounding vigorously.

Examples of the wolf's ability to persist are many (table 6.9). Even the thoroughly inbred (Wayne et al. 1991) Isle Royale wolves, whose population once dropped to 12, have persisted for 50 years (see fig. 5.6). Italy's 100 wolves of the early 1970s have quadrupled and are recolonizing France (Poulle et al. 1999). Norway and Sweden's 1 or 2 wolves of the early 1970s numbered 90–100 in 2002 (Vilà, Sundqvist et al. 2002). Some wolf populations have been beset by canine parvovirus, depredation control, sarcoptic mange, lice, poaching, hunting, trapping, snaring, snowmobile pursuit, or aerial hunting.

TABLE 6.9. Persistence histories of small wolf populations

Location	Lowest population Year	No.[a]	Current numbers	Reference
Isle Royale, Michigan	1949		29[b]	R. O. Peterson, personal communication
Mainland Michigan	1991		216	J. Hammill, personal communication
Wisconsin	1975		266	A. Wydeven, personal communication
Minnesota	1953	450–700	2,450	Berg and Benson 1999
Montana	1985		80–100	USFWS 2000
Italy	1970	100	400–500	Chapter 13 in this volume
Norway/Sweden	1978		80–95	Chapter 13 in this volume
Riding Mountain National Park	1930		40–120	Fritts and Carbyn 1995
Kenai Peninsula, Alaska	1960		150–180	Fritts and Carbyn 1995

[a] A blank cell in this column indicates that the population began in the given year.
[b] In 2000.

Nevertheless, to our knowledge, humans have not caused any wolf population to permanently decline in the last 30 years.

Important Knowledge Gaps

Despite the thousands of scientific and popular articles that have been written about wolves (Fuller 1995c; Fuller and Kittridge 1996), and despite the fact that enough information is available to formulate general guidelines for their management, many aspects of wolf biology remain to be thoroughly described (Mech 1995e). However, given financial constraints and the nature of wolf conservation problems, we have identified a more limited set of research goals that, if carried out, would improve our understanding of wolf population change. These are vital areas of investigation precisely because they are difficult to study, but advances in technology and accumulation of anecdotal information leading to testable hypotheses will greatly assist research efforts.

Dispersal and Immigration

We do not have sufficient description and quantification of movements of dispersing wolves to predict when and where wolves will go (Merrill and Mech 2000). We need to know what constitutes barriers to dispersal, and whether for wolves there are such things as dispersal corridors.

Effects of Prey Types

Wolf density and territory size seem to be affected, in part, by prey type (see table 6.3). These effects probably result from differences in vulnerability due to prey behavior, but may also be related to the habitats in which certain prey reside.

Effects of Multiple Prey

Many wolves have been studied in essentially single-prey systems, and some information is available on functional responses of wolves to changes in relative prey densities (Dale et al. 1995). However, numerical responses to such changes in multi-prey systems have only begun to be studied (Mech et al. 1998).

Multiple Breeding Females

We do not fully understand why in some packs with more than two females of breeding age, two or more produce pups, while in others, only one does (Ballard et al. 1987; Mech et al. 1998), although food abundance probably plays a strong role. The wolf reintroduction to Yellowstone National Park (Bangs et al. 1998) affords an excellent opportunity for such studies.

Role of Disease

The effects of disease on the short-term and long-term status of wolves need to be investigated. Disease is a

potentially great (e.g., Mech and Goyal 1995), but under-studied, mortality factor affecting wolf populations (see Kreeger, chap. 7 in this volume). Additional collaborative work with veterinary scientists should prove invaluable in the future.

Wolf-Human Relationships

Continual assessment of human attitudes, beliefs, knowledge, and reactions to wolf recovery and control (Kellert 1985, 1999) are essential to successful wolf conservation programs because all wildlife management is, in essence, people management. In addition, better documentation of the lack of significant population effects on wolves caused by anthropogenic disturbances (e.g., snowmobile traffic [Creel et al. 2002], hiking near den or rendezvous sites, and other recreational activities) is needed. These disturbances often are proposed as being important, but probably influence populations only when they are very widespread and intensive, if at all (Thiel et al. 1998; Blanco et al. 1992; Merrill 2002).

Population Assessment

Standardized, accurate, and cost-effective methods of assessing wolf distribution and abundance need to be identified and implemented. Future planning for and monitoring of wolf recovery, harvest, and control depends critically on unassailable population assessment techniques.

Effects of Wolves on Low-Density Prey

In contrast to our knowledge of moose-wolf population dynamics (Gasaway et al. 1992), the precise role that wolves, and other predators such as bears or humans, play in limiting deer populations at relatively low densities (e.g., Mech and Karns 1977) is poorly known (see Mech and Peterson, chap. 5 in this volume). Experiments to assess this role are difficult, and long-term studies (e.g., Mech and Nelson 2000) in several study areas may be needed.

Pup Survival

Almost 30 years ago, Keith (1974) concluded that "the factors which produce [wolf pup] mortality during the first 5 months are almost wholly unknown. This is probably the single greatest enigma in wolf biology today." Though some strides have been made toward identifying these factors, this is still a much needed area of research.