

DYNAMICS OF ISLE ROYALE WOLVES DURING A CHRONIC POPULATION DECLINE,
1987-1993

by Rolf O. Peterson, School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931; author(s) to be designated after review by National Wildlife Health Research Center, U.S. Fish and Wildlife Service, 6006 Schroder Road, Madison, WI 53711; and Joanne M. Thurber, School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931

Abstract: The ecology and demography of wolves in Isle Royale National Park, Michigan, were examined during a sustained and unexpected population decline. After a population crash in 1981-1982 that Peterson and Page (1988) attributed to food shortage, wolves continued to decline in 1984-1988 because of unusually high mortality. When high mortality abruptly ceased >1988, however, poor reproductive success prevented recovery of the wolf population. Disease screening initiated in 1988 revealed the final stages of canine parvovirus (CPV-2) occurrence in the population, a new disease that likely arrived by 1981. Disease probably played an important, previously unrecognized, role in the wolf population crash of 1981-1982 and may have contributed to subsequent high mortality through 1987, but there was no evidence of disease involvement in reproductive failure in 1989-1993. There was little support for hypotheses linking the wolf decline to relative food shortage or random demographic fluctuations. Wolf genetic characteristics support the hypothesis that reproductive success in

this isolated population declined because of inbreeding depression, exacerbated by a population bottleneck in 1982, high mortality in 1981-1988, and unequal reproductive success among alpha wolves both before and after the crash. By 1993 the population was at a precariously low level, with greatest extinction risks being the random elimination of one sex and a new cycle of disease.

Key words: Canis lupus, Alces alces, predator-prey, disease, ecology, genetics

Based on their updated chronology of the wolf (Canis lupus) population isolated in Isle Royale National Park in Lake Superior, Peterson and Page (1988:97) concluded that "...the only natural limits to wolf density are those ultimately imposed by food supply." Specifically, they attributed a major crash of Isle Royale wolves in 1981-1982 to food shortage. They predicted that wolves would remain at a relatively low level through the 1980s, then increase as the number of old moose in the population rose in the 1990s. Wolves on Isle Royale are isolated geographically from mainland wolf populations, and there is no evidence of successful immigration of breeding individuals after the population was founded in the late 1940s (Wayne et al., 1991). This wolf population was effectively protected from all human-induced mortality, and has existed in dynamic equilibrium with moose (Alces alces), its singularly important prey (Peterson et al. 1984a).

Peterson and Krumenaker (1989) acknowledged that the wolf population did not, in fact, remain stable in the late 1980s, but

declined further, and they set forth 3 hypotheses that might explain the decline: lack of food, disease, and genetic deterioration. A comprehensive list of hypotheses should include demographic stochasticity as a fourth potential cause of the wolf decline.

In 1988 the National Park Service chose to depart from a long-standing tradition of study by observation only, and for the first time allowed live-capture and radiocollaring of wolves on Isle Royale. A period of intensified monitoring followed, to better evaluate possible causes of the wolf decline and to document an ongoing natural experiment in small population viability. Here we present, as a sequel to Peterson and Page (1988), a summary of wolf ecology and demography during 1987-1993, when the population fell to its lowest level since its establishment in the late 1940s.

STUDY AREA AND METHODS

Isle Royale is a roadless island (544 km²) in Lake Superior, located about 25 km from the Ontario mainland. It is almost entirely forested, with a mix of boreal and mixed hardwood tree species (Peterson 1977). Wolves on Isle Royale subsist primarily on moose, with beaver (Castor canadensis) as a secondary prey that may be seasonally important (Mech 1966, Peterson 1977, Peterson and Page 1988, Thurber and Peterson 1993). Almost the entire island is managed by the U.S. National Park Service as a designated Wilderness Area, and human activity is largely limited to shoreline campgrounds and a 280-km system of foot trails. After 1978 mammalian pets were not permitted on the island. The park is

staffed and open for visitation only from mid-April through October.

During 1987-1993 field studies of wolves were conducted annually during 2 periods, a winter study of 50 days beginning in mid-January, and a summer study usually commencing in mid-May and extending through August. During the winter study wolves were snow-tracked, counted, and observed from light ski-equipped aircraft (Piper Aircraft 18-150 Supercub). A complete count of all wolves was made several times in each winter study. Wolves, especially territorial packs, were back-tracked in snow to determine the extent of their travels. These packs usually occupied exclusive, defended space, and scent-marked regularly during their travels (Peters and Mech 1975). In summer wolves were radio-tracked from aircraft and on foot, and frequently-used sites were monitored for evidence of reproduction.

During 1988-1993 wolves were live-captured using custom-built Newhouse-type 14 leghold traps (Kuehn et al., 1986) or a similar commercially-available trap (Rancher's Supply, Alpine, TX). Traps were checked daily and captured wolves were anesthetized for handling (Thurber and Peterson, 1993). Wolves were weighed, blood-sampled for disease screening and genetic studies (Lehman et al., 1991; Wayne et al. 1991), and released wearing motion-sensitive radiocollars (Telonics, Inc., Mesa, AZ). Parasite load and disease incidence was determined by direct external examination and subsequent laboratory studies of blood and feces. Antibodies to canine parvovirus (CPVII) were determined by the hemagglutination

inhibition (HAI) test (Thomas et al. 1984). Serial dilutions of serum were tested, and the HAI titer was determined to be the reciprocal of the highest dilution at which HAI activity was evident. Wolf tissues from live-captured wolves and carcasses of dead wolves recovered intact were examined at the Wildlife Health Research Center, U.S. Fish and Wildlife Service, Madison, WI, together with cooperating investigators and other laboratories.

Wolves were tracked daily by aircraft during the winter study and 1-2 times/month in summer. Traditional or suspected den sites and rendezvous areas were examined on the ground in summer, and pups were counted opportunistically during group howls. Pups were more accurately enumerated in winter by direct observation from aircraft of wolf behavior and appearance (Peterson and Page 1988), using a 15X gyro-stabilized monocular viewing device (Fraser-Volpe, Inc., Warrington, PA). Annual mortality was estimated from total population size and the number of new recruits each winter, assuming zero emigration and immigration. The winter study usually encompassed the entire period when an ice connection from Isle Royale to the mainland might have allowed movement.

During the annual winter study, alpha (dominant) wolves were individually recognizeable within each year, and these wolves could often be distinguished in successive years on the basis of physical appearance. Female wolves in breeding condition were identified by vaginal bleeding evident in snow-urine, and those in breeding condition were considered potential reproducers if they were actively courted by a male.

RESULTS

Prior to this study the Isle Royale wolf population fluctuated between 14 and 50 wolves, and average population size was 27 during 1959-1986 (Jordan et al., 1967; Mech, 1966; Peterson, 1977; Peterson and Page, 1988; Wolfe and Allen, 1973). The population was stable in 1959-1973, then it increased steadily to reach a peak in 1980. A population crash in 1981-1982 left only 14 wolves alive, but the population recovered to 20 wolves or more during the mid-1980s (Peterson and Page, 1988). The crash of 1981-1982 provided a natural discontinuity or breakpoint for analysis of demographic parameters over time.

Wolf Numbers and Organization

Wolf population size declined from 20 in 1986 (Peterson and Page 1988) to 16 in 1987 and 12 in 1988, the lowest level attained since annual counts were initiated in 1959 (Table 1). Thereafter the population stabilized, and 13 wolves were present in 1993 (Fig. 1). Mean annual fluctuations in population size, indicated by finite rate of increase (λ , Caughley 1977:51), were slightly lower after the 1981-1982 crash (1959-1979 median $\lambda = 1.07$ vs. 1983-1992 median $\lambda = 0.96$, Mann-Whitney test, $P = 0.067$).

In each winter the wolf population was consistently partitioned into 2-3 social groups, territorial packs that exhibited scent-marking by alpha wolves. These packs typically occupied territories for several years, and areas used by new packs (EIII pack in 1989, MII Pair in 1990) were usually similar to territories of previous packs that disappeared (Table 1, Fig. 2).

In such cases it was possible that a single uncollared alpha wolf remained as a founder of a subsequent pack.

Wolf packs often chased and occasionally killed non-pack wolves within their group territory. The outcome of encounters between packs and single wolves was highly varied and partially dependent on individual circumstances and previous associations (Appendix A). In one case a chase of a lone wolf by the West II Pack (WII) was followed 2 days later by a fatal attack on the same wolf. Another lone wolf was chased at least twice by this pack but not attacked. After reproducing successfully, one alpha female became intolerant of another female and threatened her during a chase and a non-fatal attack, even though the 2 wolves had previously been close associates.

The WII pack, with an origin no later than 1982, was the only pack to persist throughout 1987-1993. The EII pack declined to just an alpha pair by 1988 and may have persisted in 1989, but by 1990 a new pack (EIII pack) had replaced it and assumed the same territory. The Harvey Lake (HL) pack, persecuted for many years by both neighboring packs (Peterson and Page 1988), continued as a remnant group of 3 wolves in 1987 after a fatal attack by the EII pack in 1986. In 1987 the EII pack again attacked the HL pack, and this time the alpha male was killed. The remaining female and a possible pup did not scent-mark, and their former territory was utilized by the EII and WII packs in 1988 and 1989. In 1990 a yearling male dispersed from the WII pack (550) and paired with a female of unknown origin, and they claimed a territory in the

middle of the island in 1991-1993.

Reproduction

Wolf pups were accurately counted only during the annual winter study, after they reached the age of 8 months (Table 2). The number of annual pup recruits steadily declined during 1983-1993 (Fig. 3). In 1984-1993 median annual pup production for the population was only 3.0, compared to 8.0 in 1971-1980 (Mann-Whitney test, $P = 0.009$). The earlier counts were minimal estimates (Peterson 1977:114) while the later counts (with a stabilized viewing device) were considered more accurate.

Average litter size declined only slightly after the 1981-1982 crash and it was highly variable in both periods (median 2.2 in 1984 - 1993 vs. median 3.0 in 1971-1980; Mann Whitney test, $P = 0.16$). Before the crash every breeding alpha female bore young each year, but > 1985 actual reproduction increasingly fell short of potential reproduction set by the number of females in breeding condition (Fig. 4).

There were only 2 years during 1971-1993 when no pups were present in the winter population, 1982 and 1990. In 1981 at least 9 pups were alive in August, distributed in 3 packs, while in 1989 no pups were detected during summer.

Based on reproduction in packs with alpha wolves that were individually recognizeable, it was clear that variation in lifetime reproduction was substantial. Specifically, only a few individuals bore a disproportionately large number of recruits. During 1971-1993, 137-147 pups were identified in winter counts. Approximately

two-thirds (61-69%) of these pups were produced by only 4 alpha wolves (Table 3). Three of these wolves produced 73-84% of the 88-96 pups born before the crash, while 1 alpha male sired 39-41% of the 49-51 pups born after the crash.

Mortality

In 1971-1993 the annual number of deaths among wolves counted the previous winter was <10 except in 1977 and 1981-1982 (Fig. 3). Approximately 17 wolves disappeared between successive winter studies in 1976 and 1977, but an exceptional ice connection to the mainland in 1977 permitted wolf travel to the mainland (Peterson, 1979). Between the counts in 1980 and 1982, when no ice bridge to the mainland existed, 42 wolves died that had been previously counted in winter. An additional 9 pups alive in summer 1981 also perished. Starvation of old wolves and direct killing by other wolves were documented causes of death for a small number of dead wolves recovered in this period (Peterson and Page, 1988).

Mean annual mortality for the population was $23.4 \pm 3.6\%$ (SE) during 1971-1993 (Fig. 5), including a period of consistently high mortality in 1981-1988, when mean annual mortality was $41.0 \pm 3.5\%$ (SE).

Of the 20 wolves that were alive during any portion of 1988-1993, 9 had died by August 1993. Presumed causes of death included killing by other wolves, accidents, and emaciation (Table 4). Aside from opportunistic recovery of carcasses of wolves killed by other wolves, the only notable individual record of mortality during the period of highest mortality (1981-1988) involved a pup

that died in 1986 in the WII pack. Its skeleton was recovered a year after death in a dense thicket of vegetation near a rendezvous site. From skeletal size its whole body weight was estimated at 20 kg, suggesting mortality between August and October. There was little direct information on mortality factors for most of the wolves that died in 1981-1988.

Individual data, sex ratio

Eleven wolves, all > 1 yr old, were handled during 1988-1993, including 9 of the 12 wolves in the population in 1988 (Table 5). Mean body mass was 32.6 ± 1.6 (SE) for 5 females and 39.7 ± 2.3 (SE) for 6 males.

Nipple development on females (Mech et al. 1993) suggested that only 1 female (600) we handled had reproduced. This female was nursing young in the territory of the EIII pack when captured in Aug 1989, but in Jan 1990 female 450 led 3 pups in this territory and female 600 lived as a lone wolf within EIII pack territory and often followed this pack. By 1991 female 450 was the only reproducing female in the population, and she raised 2 pups in both 1991 and 1992. Alpha females in WII pack and the MII pack were in estrous each February and each probably mated with the respective alpha male, but pups were not detected in these packs in either summer or winter.

By August 1993 the 12 wolves remaining on Isle Royale included 3 females, 7 males, and 2 wolves of unknown sex. Each of 3 territorial packs contained an α female in breeding condition.

Disease status

Four wolves handled in 1988 were thoroughly screened for endo- and ecto-parasites and diseases of viral, bacterial, and fungal origin. No evidence was found of rabies, canine distemper, brucellosis (Brucella spp.), leptospirosis (Leptospira spp.), blastomycosis, heartworm (Dirofilaris immitis), the dog louse (Trichodectis canis), or mange (Sarcoptes scabiei). All 4 wolves tested positive for infectious canine hepatitis, a common condition for wild wolves in North America (Zarnke and Ballard 1987). Inconsistent laboratory results for Lyme disease (borreliosis, caused by Borrelia burgdorferi) were obtained, and there were no clinical indications of Lyme disease.

Two of the first 4 wolves handled in 1988 exhibited antibodies for CPV-2 (both had HAI titers of 320), based on consistent results from 3 independent labs (Table 5). In 1989, 2 of 4 wolves were marginally positive for CPV-2, including 1 recaptured wolf that was negative in both 1988 and 1989. In 1990-1993 the remaining 4 wolves were all negative for CPV-2. Serological testing of 31 red foxes (Vulpes vulpes) caught on Isle Royale incidental to wolves in 1988 and 1989 revealed no positive titers for CPV-2 in this species.

Fresh fecal samples from 4 captured wolves and 13 others collected throughout Isle Royale in 1988-1990 were examined microscopically for parasites. Evidence of helminth parasites was found in 13 of the 17 fecal samples. One sample contained 3 species of helminth parasites, 3 other samples contained 2 species each, and 1 helminth species was identified in 9 samples. The

highest species prevalence was for hookworm (probably Uncinaria spp.), indicated by strongyle eggs and first-stage hookworm larvae, in 12 of the 17 samples. Taeniid eggs were found in 3 samples, and 1 sample was identified with each of the following: Filaroides spp., Trichuris spp., and Alaria spp., and Eucoleus aerophilus. Upon necropsy a complete examination of the gastrointestinal tract of 1 emaciated wolf with heavily-worn teeth revealed a heavy infection of Echinococcus granulosus.

DISCUSSION

The population crash and subsequent chronic decline of Isle Royale wolves during 1981-1988 coincided with a period when annual mortality ranged from 27-54%. Wolf populations usually cannot annually replace losses >30% (Keith 1983, Peterson et al. 1984b), so the decline of Isle Royale wolves was clearly linked to a period of sustained high mortality. Beginning in 1985 failure to recruit pups, together with a slight decline in the annual number of recruits raised in reproducing packs, increasingly became an important limiting factor for the population. During 1988-1993 both reproduction and mortality were very low, and the population stabilized at its lowest documented level. It is unlikely that any single factor was responsible for the observed changes, overlapping but asynchronous, in both mortality and reproduction. Possible influential factors will be discussed in the context of 4 hypotheses that individually specify demographic stochasticity, food shortage, disease, and genetic losses as the primary driver of wolf population change.

Did random fluctuations in wolf demography, perhaps forced by environmental stochasticity, play a role in the wolf decline? For small populations, both demographic and environmental stochasticity may influence population level and, hence, persistence time (Ballou et al. 1989). Wolf demography on Isle Royale clearly had an environmental link (food supply) in 1959-1980 as wolf numbers closely followed trends in the number of old moose, their predominant prey (Chap. 8). Age structure of moose, a long-lived prey, changed only slowly over time. During 1959-1979 there was relatively little random noise in wolf reproduction or mortality, except in 1977 when emigration may have caused a high loss of individuals. Neither the high mortality that prevailed in 1981-1988 nor the steady decline in reproductive success in 1985-1993 appeared to be random fluctuations, but rather unprecedented demographic responses to new ecological conditions.

Individual idiosyncracies, a form of stochasticity, could be of demographic significance in a very small population. By 1993 all 3 alpha females in territorial packs appeared to be quite old (indicated by progressively lighter pelage on head and sides). The only reproducing female (450) was estimated to be 4-8 years old in 1988, thus 9-13 years old in 1993. Could reproductive success of the population have declined simply because of advancing age in a small number of potential breeders? During 1985-1993 there was turnover in at least 1 alpha wolf in each of 3 territorial packs--the WII pack recruited a new alpha female in 1987 and a new alpha male in 1988 (421), the MII pack recruited a new alpha male (2-yr-

old 550) in 1990 (though the alpha female could have been old), and the EIII pack recruited a new alpha female (450) in 1989 or 1990, who became mated to a male (410) that had sired 3 pups in 1989. Advanced age is an unlikely explanation for uniformly poor reproductive success in the population.

We emphasize that our best annual measure of reproductive success was in winter, when pups were 8-9 mo. old, although in summer minimum estimates of pup occurrence in each pack were usually possible when pups were 2-4 mo. old. Wolf pups that perished <2 months after birth were undetected by our field surveys. If pups succumbed to CPV-2 (the only disease of inferred significance), we would expect mortality after weaning at ca. 3 months of age, when young wolves would no longer be protected by maternal antibodies (C. Parrish and J. Zuba, pers. commun.). Indeed, the skeleton of an Isle Royale pup that died in 1986 was of a size that suggested mortality at ca. 4 months of age. In 1981, when we speculate CPV-2 was responsible for high mortality, at least 3 pups were detected in each of 3 packs in August, but none were subsequently present during aerial surveys in January. Lack of detection of pups in our field surveys suggests that reproductive failure occurred some time between conception and the early post-natal period.

Was a relative food shortage influential at all during 1981-1993? This question can be addressed using comparative results from other wolf populations and correlative historic data from Isle Royale. Mean per capita prey availability for Isle Royale wolves

during 1959-1980 (before the 1981-1982 crash) was 41 (SE = 3.6) moose, close to the "global" regression equations linking wolf density to moose density (45, 42, and 27 moose/wolf, respectively, from Fuller, 1989; Gasaway et al., 1992; and Keith, 1983). These extensive data sets include a wide variety of ecological conditions, none characterized by chronic reproductive failure in resident wolf populations.

We point out, however, that even during 1959-1980, when wolf numbers appeared to be tracking food supply, the size of the wolf population could not be accurately predicted from moose population size ($P = 0.346$, $R^2 = 0.00$), raising serious doubts about the predictive value of ratio dependency for a single wolf-prey system. The number of old moose (>9 yr old), however, which constitute most wolf-kills, was an adequate predictor of wolf density for 21 years ($P < 0.001$, $R^2 = 0.74$, Fig. 6). During this period the average number of available old moose per wolf was 8.0 (range 3.9 - 10.7, SE = 0.4) and wolf reproduction was consistently maintained in territorial packs. During 1985-1993, with recurring reproductive failure, the average number of old moose per wolf was 17.4 (SE = 1.3) and was never lower than 10.1. Thus the available data on abundance of wolf prey at Isle Royale provide no support for the food shortage hypothesis.

Messier (1987) found that wolves preying on low density moose populations (0.2 moose/km²) had lower success in producing pups, but still did so in 61% of the possible occasions; where moose density was higher (0.4 moose/km²), 93% of the wolf packs

reproduced. At Isle Royale in 1985-1993, with moose density >2.0 moose/km² and 3-4 territorial breeding pairs present, successful reproduction occurred in only 47% (N = 47) of the possible occasions. This represents unprecedented lack of reproduction for wild wolves, with no evident explanatory linkage to prey.

There appear to be no disease agents identified for wolves that would explain the specific circumstances surrounding reproductive failure for Isle Royale wolves. Parasites and diseases, however, may limit wolf survival in some cases (Brand et al. 1994). We believe that CPV-2 is the only disease that might have been of demographic importance during the decline of Isle Royale wolves, even though direct evidence of mortality from CPV-2 was lacking. CPV-2 was shown to be quite virulent in wolves upon first exposure, responsible for death of 11 of 12 pups and yearlings in a captive pack (Mech and Fritts 1987). Mech and Goyal (1993) found correlative evidence linking wolf population trend with prevalence of CPV-2 in Minnesota, and he felt that in an enzootic stage CPV-2 might be responsible for significant pup mortality.

Positive CPV-2 titers were only found in Isle Royale wolves in 1988, the first year of testing. This established that CPV-2 was concurrently or formerly present at Isle Royale, and we presumed that CPV-2 probably caused extensive mortality when this naive food-stressed population was first exposed to this disease. After its first appearance in domestic dogs in 1976 or 1977, CPV (a new mutant, CPV-2, first appeared in 1980, according to Parrish et al.,

1991) was clearly present in other North American wolf and coyote populations by 1979 and 1980 (Brand et al., 1994; Bailey et al., 1994). In summer, 1981, there was a local outbreak of CPV-2 among dogs in Houghton, MI, a mainland point of departure for visitors to Isle Royale. CPV-2 probably arrived at Isle Royale in 1979-1981, just prior to unprecedented mortality of all wolf pups in the 1981 cohort and high losses among older wolves in both 1980 and 1981. While the available evidence is entirely circumstantial, we believe it points to a significant role for CPV in the population crash of Isle Royale wolves in 1981-1982. CPV is not so readily linked to subsequent mortality in 1983-1988, even though the lack of positive CPV titers after 1988 coincided with a cessation of mortality in 1988.

Limited evidence suggests that Isle Royale wolves support an extensive array of helminth parasites. Individuals with heavy parasite loads might be prone to higher mortality from food shortage, disease, or normal aging, but we have no information on possible temporal changes in parasite occurrence. We speculate that heavy parasite loads might have predisposed adult wolves at Isle Royale to mortality from CPV-2, as the continuing high turnover of wolves >8 months old during 1982-1988 is not readily explained by results of experimental single-factor studies of CPV-2 infections in canids, where only pups were found to be highly susceptible (Meunier et al. 1981, Parrish et al. 1982).

The genetic characteristics of Isle Royale wolves support the hypothesis that inbreeding depression led to progressively greater

reproductive failure in the late 1980s and early 1990s. There are several factors that might have influenced the appearance of genetic problems for this isolated population. First, the 1981-1982 crash produced a genetic "bottleneck" by eliminating most wolves in the population. Subsequently, even though reproducing alpha wolves may have been long-lived, high mortality among other wolves during 1983-1988 extended the bottleneck effect for several additional years.

Finally, uneven reproductive success arising from variation in lifespan of alpha wolves probably influenced the rate that genetic heterozygosity was lost from the population. Genetic variation in a small population would be maximized if each individual had an equal opportunity to breed, and if each breeder lived as long as possible. Where mating opportunities are restricted to long-lived alpha wolves, their presence might over time lead to progressively greater genetic uniformity in the population by eliminating opportunities for other adults to reproduce. Yet wolves with exceptionally long tenure in an alpha position will forestall the passage of generations, thereby reducing the rate of loss of heterozygosity. Long-lived alpha wolves at Isle Royale were probably replaced by wolves from a subsequent generation, but the average tenure of most alpha wolves was only 2-4 years. We have no data on origin or age of wolves that assumed alpha positions of average duration. If these alpha wolves were also typically replaced by individuals from a later generation, then the observed long tenure of alpha wolves at Isle Royale effectively forestalled

genetic problems until high mortality and rapid turnover removed this buffer.

The wolf population at Isle Royale, representing a prominent population but one considered non-essential for species survival, will for the present be left unmanipulated as a test case in small population viability. Restoration may proceed after functional extinction, as in the case of total loss of one sex, or cessation of reproduction. Another outbreak of virulent disease is also an important potential extinction risk. The short-term future of this population will likely be determined by random events.

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Table 1. Isle Royale wolf numbers and organization, 1987-1993.

Year	Territorial packs					Size of other groups		Total
	EII	WII	HL	EIII	MII	2	1	
1987	4	8	31	-	-	-	1	16
1988	2	6	-	-	-	1	2	12
1989	2 ¹	3	-	3	-	1	2	12
1990	-	2	-	5	2	1	4	15
1991	-	2	-	4	2	1	2	12
1992	-	2	-	5	2	-	3	12
1993	-	2	-	7	2	-	1	13

¹Pack occupied same territory as previous year, but identification was uncertain.

Table 2. Estimated reproduction and mortality for Isle Royale wolves, 1971-1993.

Year	Winter count	No. litters	Total pups ¹	Mean pups per litter ¹	Annual mortality (%)
1971	20	1	2	2.0	0 (0/18)
1972	23	2	10 ²	5.0	35.0 (7/20)
1973	24	2	7	3.5	26.1 (6/23)
1974	31	2	8	4.0	4.2 (1/24)
1975	41	3	15 ³	4.8	14.5 ^{3,4} (4.5/31)
1976	44	3	10-12(s)	2.8-3.5	13.4 ³ (5.5/41)
1977	34	3	8-9(s)	2.1-2.5	37.5-39.8 ³ (16.5-17.5/44)
1978	40	4	9-10 ⁵ (s)	1.9-2.1	4.4-7.4 (1.5-2.5/34)
1979	43	4	9-10 ⁵ (s)	1.9-2.1	11.3-13.8 (4.5-5.5/40)
1980	50	4	9-12 ⁵ (s)	2.4-3.1	5.8 ³ (2.5/43)
1981	30	3	7 ⁵ (s)	2.3	54.0 ³ (27/50)
1982	14	3	0	0	53.0 ³ (16/30)
1983	23	4	13	4.3	28.6 (4/14)
1984	24	3	10-11	3.3-3.7	39.1-43.5 (9-10/23)
1985	22	2	7	3.5	37.5 (9/24)
1986	20	2	4	2.0	27.3 (6/22)
1987	16	2	4-5	2.0-2.5	40.0-45.0 (8-9/20)
1988	12	1	3	3.0	43.8 (7/16)
1989	12	1	1	1.0	8.3 (1/12)

Table 2 (cont'd)

Year	Winter count	No. litters	Total pups	Mean pups litter ⁻¹	Annual mortality (%)
1990	15	1	3	3.0	0 (0/12)
1991	12	0	0	0	20.0 (3/15)
1992	12	1	2	2.0	16.7 (2/12)
1993	13	1	2	2.0	8.3 (1/12)

¹Pups present in winter unless only summer (s) count was available; in the latter case the winter estimate equaled the summer count minus 0.5 pups per litter (Peterson and Page, 1988). Midpoint of intervals used to calculate annual means.

²Pup numbers unknown, value for the same pack from adjacent year used (for West pack in 1978 and 1979, 1-2 pups, the 1977 winter level; for Harvey Lake pack in 1978 and 1979, 2 pups, the 1980 winter level; for Middle and East packs in 1979, 3 pups each, the 1977 summer level; for West pack in 1972, 4 pups, the 1973 winter level).

³Five pups each counted in WII and Middle packs in winter, 5 observed in previous summer in EII pack.

⁴Corrected from Peterson and Page (1988:94).

⁵Pups recorded in summer except for HL pack, which contained 2

pups and 1 pup in winter, 1980 and 1981, respectively. This pack was assumed to contain 2 pups in winter, 1978 and 1979.

Table 3. Alpha wolves on Isle Royale with unusually high reproductive success 1971-1993¹.

Wolf #	Pack	Winter	No. surviving
		Period	offspring ²
Female 2	East	1972-1981	35-37
Female 3	West	1973-1976	17-18
Male 7	East	1975-1979	19-20
Male 11	West II	1982-1987	20

¹The remaining identifiable alpha males (N = 11) and females (N = 7) produced an average of 5.2 (SE = 0.7) offspring during their tenure as a pack leader.

²Pups identified in winter surveys at an age of ca. 8 mo.

Table 4. Individual status¹ of all wolves on Isle Royale, 1988-1993.

Wolf	Sex	Pack	Year						Comments
			1988	1989	1990	1991	1992	1993	
450	F	450	A	A ²	A ²	A ²	A ²	A ²	Alpha wolf
410	M	450	A	A	A	A	A	A	Alpha wolf
430	M	450	-	-	A	A	A ²	A ²	Dispersed at age 4 yr
A	?	450	-	-	A	A	D	D	Dispersed at age 1-2 yr, died 1992, unknown cause
B	F	450	-	-	A	A	A	A	Dispersed at age 2-3 yr, killed in Feb 1992 by WII pack
C	?	450	-	-	-	-	A	A	Remained in natal pack at age 1-2 yr
D	?	450	-	-	-	-	A	A	Remained in natal pack at age 1-2 yr
E	?	450	-	-	-	-	-	A	
F	?	450	-	-	-	-	-	A	
G	F	WII	A	A	A	A	A	A	Alpha wolf
421	M	WII	A	A	A	A	A ²	A ²	Alpha wolf, died Jul 1993, after probable injury by moose
H	F	550	A	A	A	A	A	A	Alpha wolf
550	M	550	-	A	A	A ²	A ²	A ²	Dispersed at age 1-2 yr, became alpha wolf
470	M	--	A	A ²	A ²	A ²	A ²	A ²	Non-territorial, usually alone
670	F	--	A	A	A ²	A ²	D	D	Died Feb 1991, fell through ice ³
420	M	--	A	A ²	A ²	A ²	D	D	Died Jan 1991, emaciated (29 kg) with heavy tooth wear
490	F	--	A	A	A ²	D	D	D	Killed by WII pack Feb 1990
600	F	--	A	A	A ²	D	D	D	Died ca. Nov 1990, unknown cause ³
590	F	--	A	A ²	A ²	A ²	A ²	D	Died 1992, unknown cause
I	?	?	A	D	D	D	D	D	Died ca. Dec 1988, probably killed by moose

¹Wolf status in Jan of each year indicated by "A" (alive) and "D" (dead).²Radiocollared wolf with operating transmitter.³Wolf mortality coincided with disappearance of radiosignal.

Table 5. Chronological data for wolves live-captured on Isle Royale, 1988-1993.

Wolf	Sex	Mass (kg)	CPV-2 titer ¹	Date
450	F	34	--	Apr 29, 1988
470	M	45	++	May 1, 1988
420	M	36	--	May 1, 1988
590	F	35	++	May 3, 1988
600	F	36	--	Aug 28, 1989
670	F	27	+-	Sep 6, 1989
490	F	31	+-	Sep 18, 1989
420R ²	M	33	--	Sep 25, 1989
550	M	31	--	Aug 21, 1990
421	M	44	--	May 2, 1991
430	M	42	--	May 11, 1991
410	M	41	-- ³	May 1, 1993

¹ Canine parvovirus HAI titer considered positive (++) if > 320, marginal (+/-) at 160, negative (--) if < 160.

² Recaptured wolf.

³ To be confirmed, 12/21/93.

Figure captions

Fig. 1. Fluctuations in wolf and moose populations on Isle Royale, 1959-1993.

Fig. 2. Spatial organization of Isle Royale wolves, 1987-1993.

WII = West II pack, HL = Harvey Lake Pack, MII = Middle II pack, and EII = East II pack.

Fig. 3. Wolf reproduction and mortality on Isle Royale, 1971 - 1993. Year corresponds to annual winter study in Jan-Mar (i.e., 1976 = cohort year 1975).

Fig. 4. The number of potential and actual reproducing alpha female wolves on Isle Royale, 1971-1993.

Fig. 5. Population level and annual mortality for Isle Royale wolves, 1971-1993.

Fig. 6. Moose:wolf ratio and old moose:wolf ratio, Isle Royale National Park (Chap. 8).

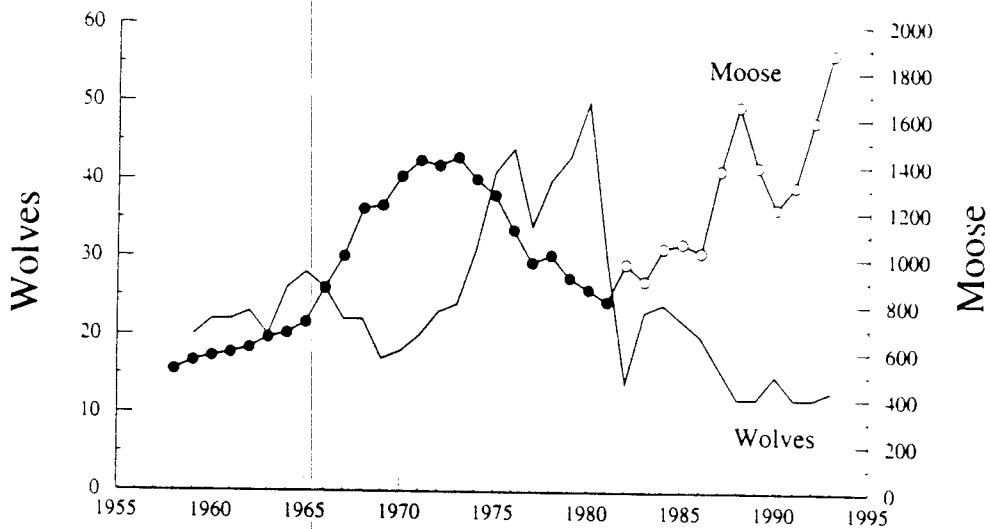


Fig. 1

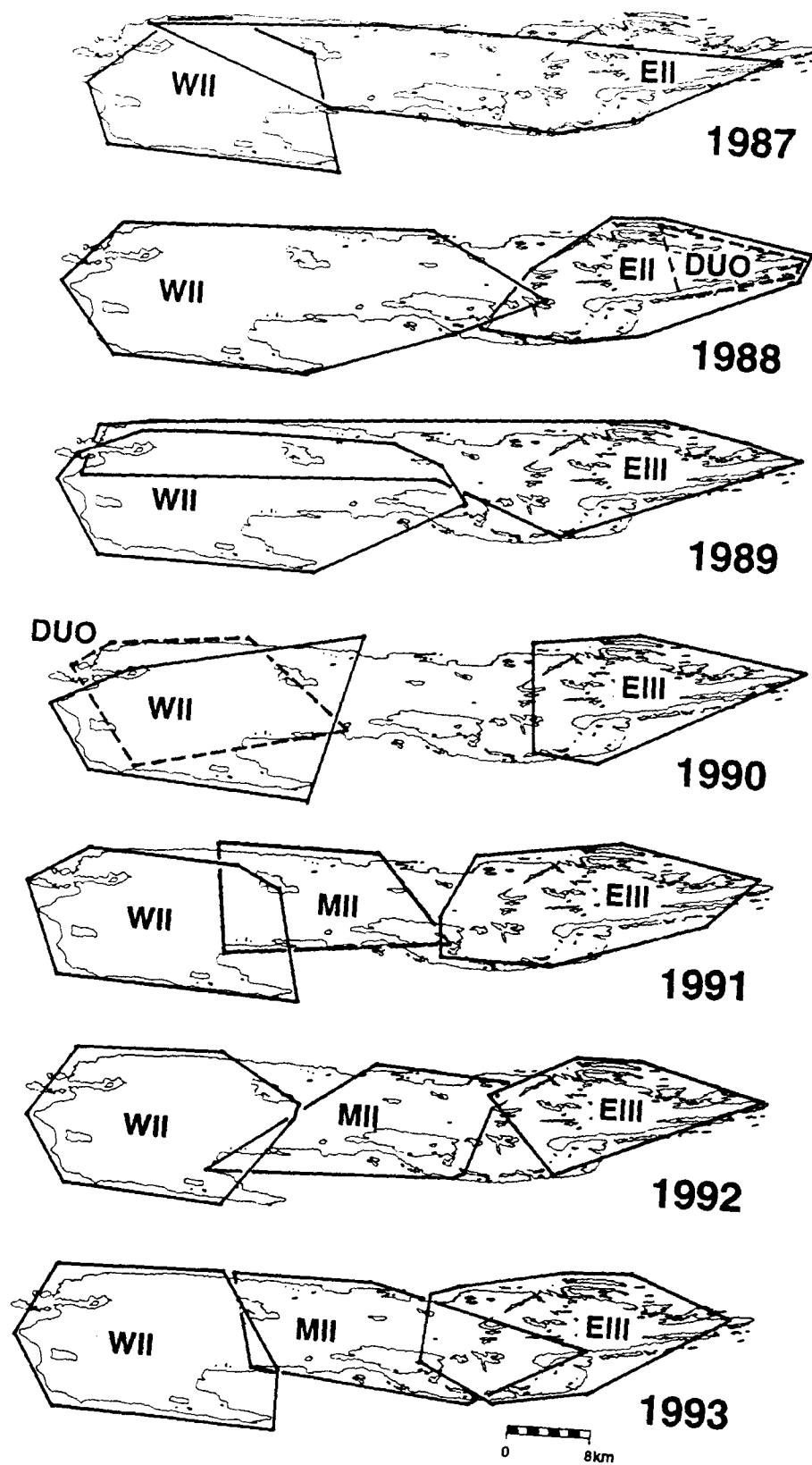


Fig. 2

Wolf demography (reproduction and mortality)

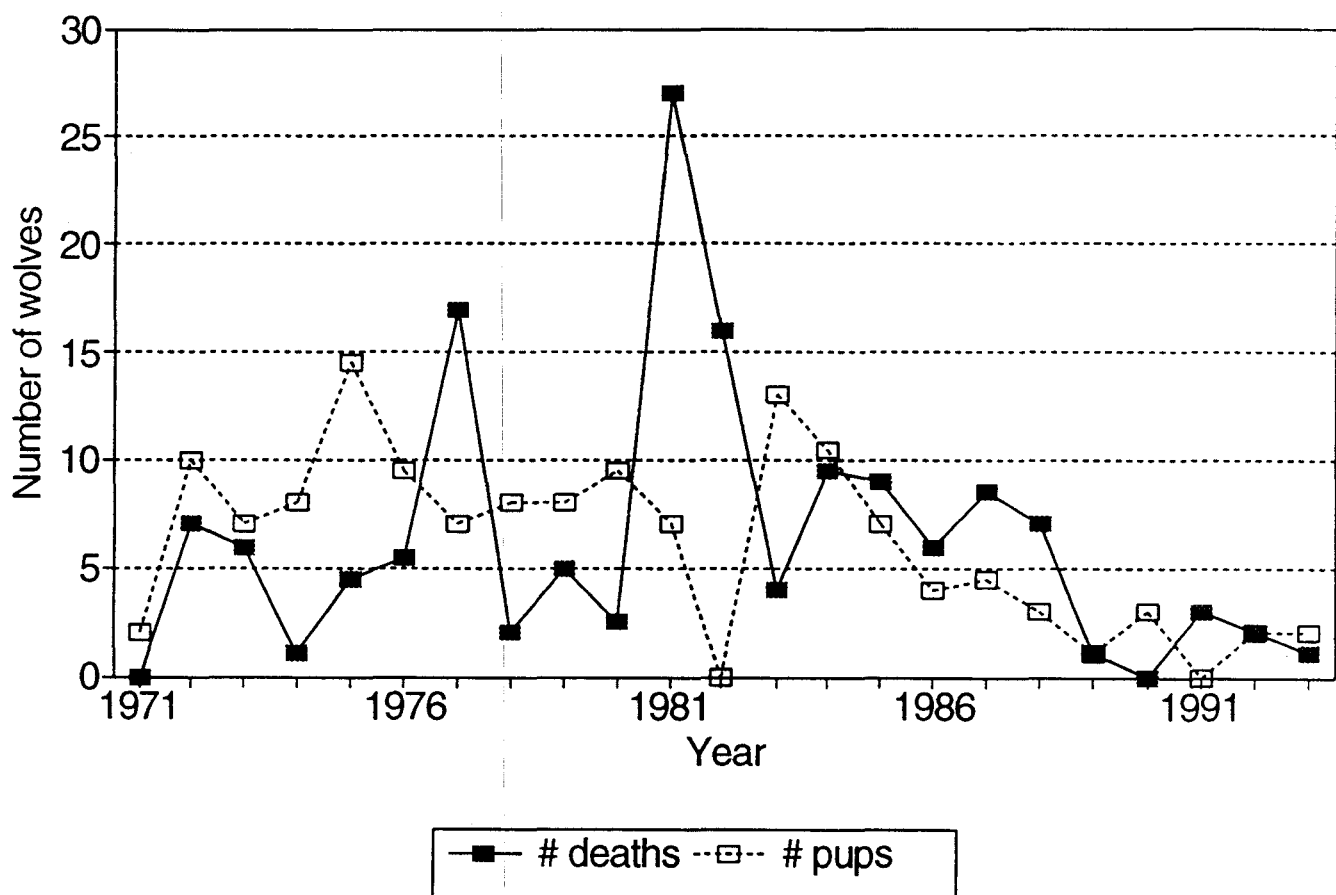


Fig. 3

Wolf reproductive success

Isle Royale National Park

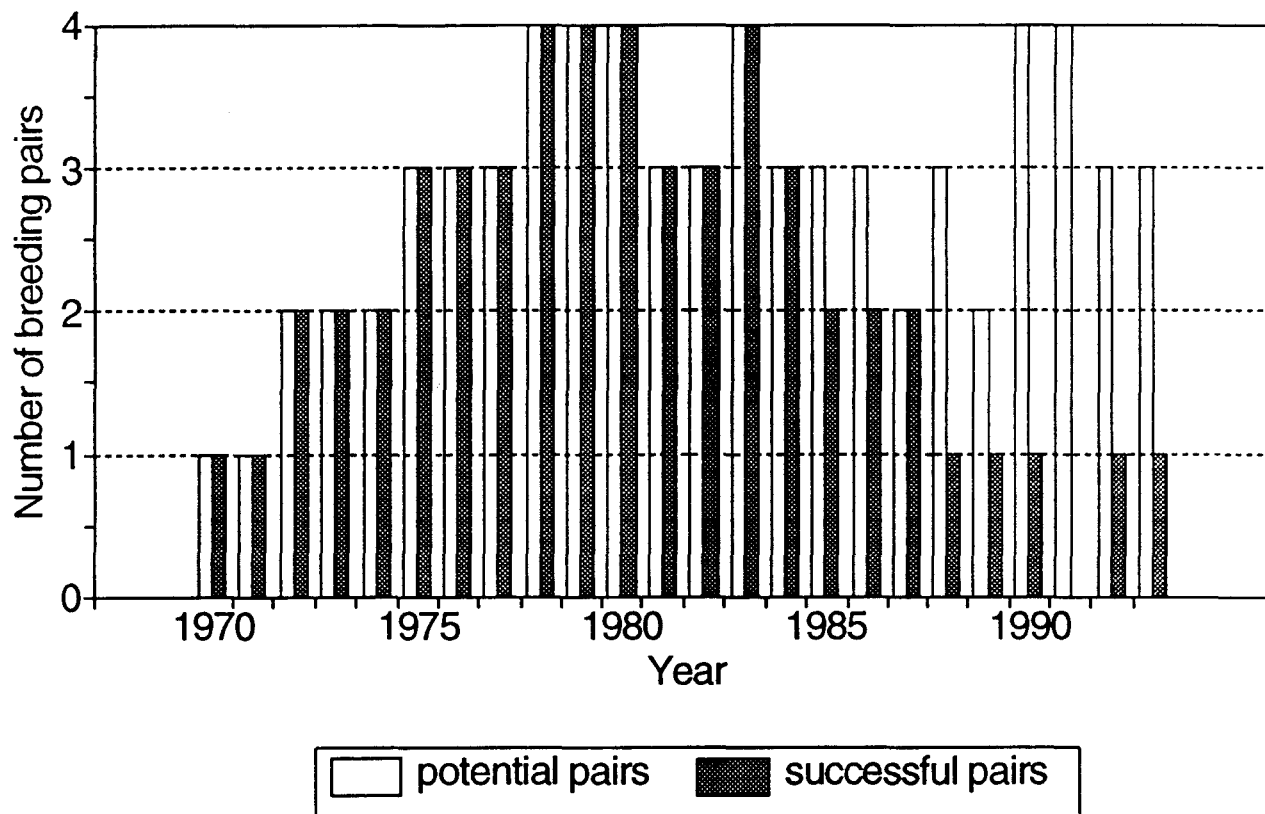


Fig. 4

Wolves on Isle Royale

(population size & mortality)

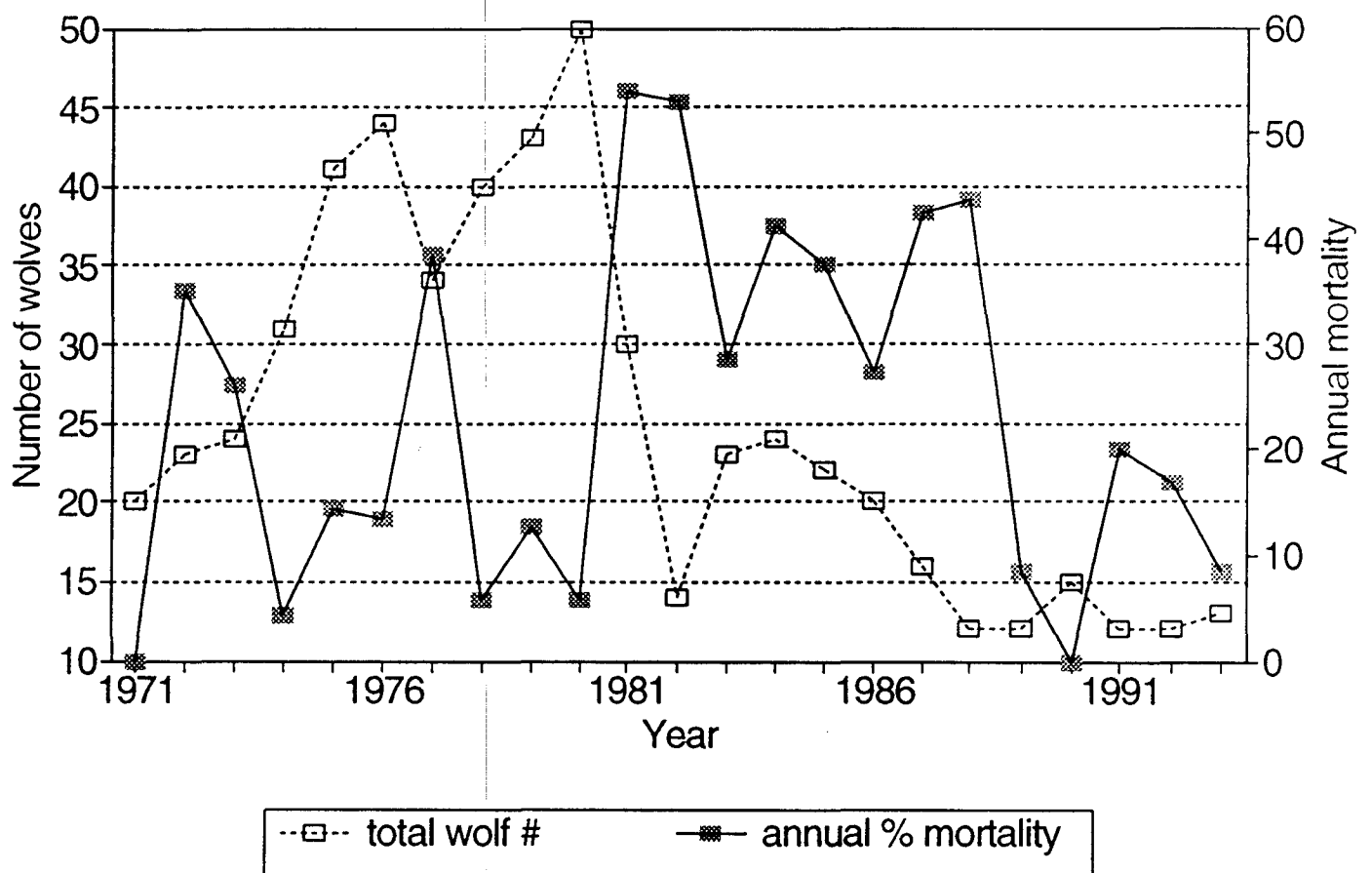


Fig. 5

Prey:wolf ratio

Isle Royale National Park

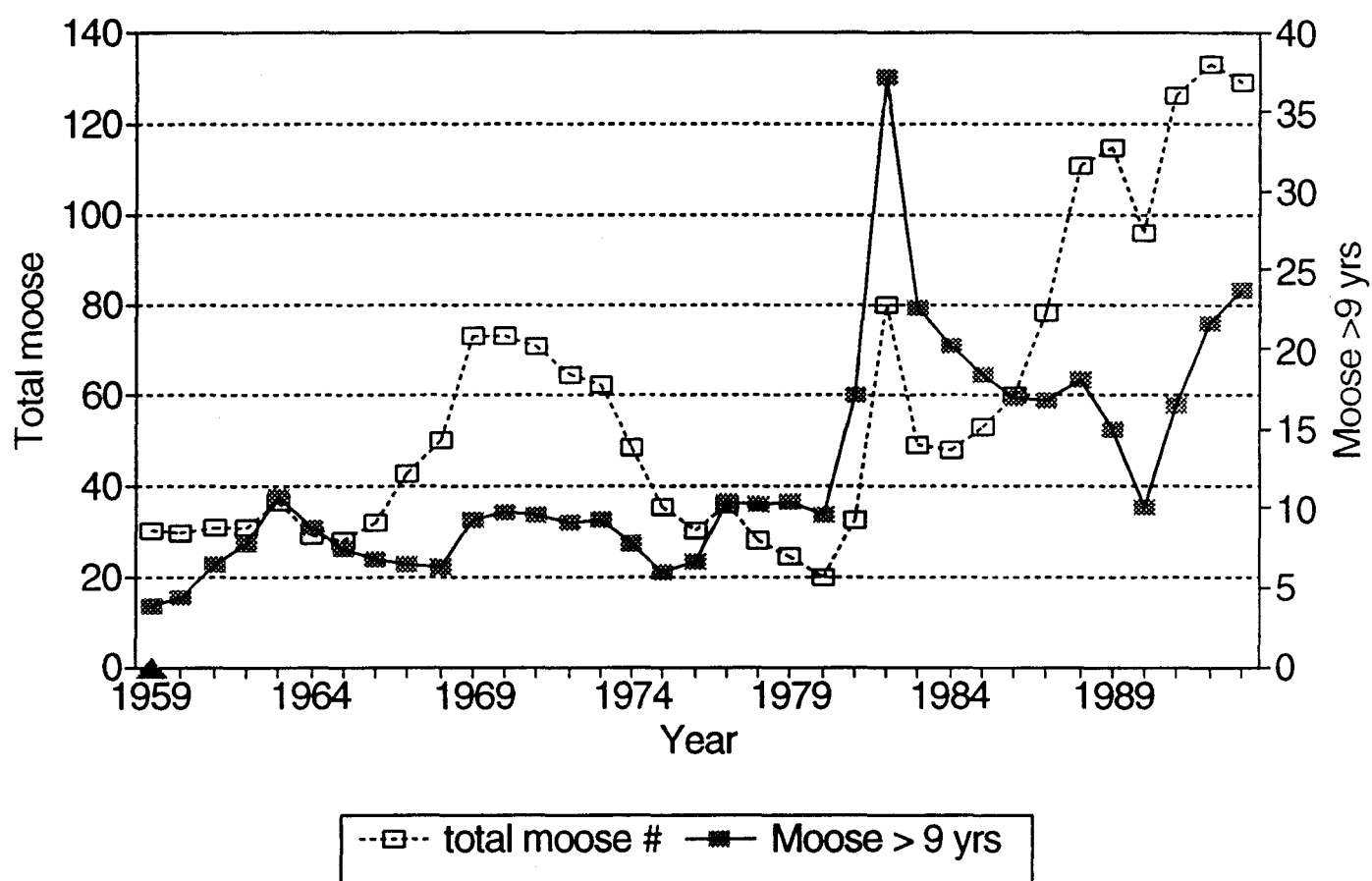


Fig. 6