

WOLF POPULATION DYNAMICS AND PREY AGE STRUCTURE IN ISLE ROYALE
NATIONAL PARK

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Abstract: At large spatial and temporal scales wolf density is broadly correlated with prey density (Gasaway et al. 1992), consistent with expectations for a top carnivore. Yet during a 2-decade period annual fluctuations of wolf numbers in Isle Royale National Park were not similar to fluctuations in moose, their primary prey. Moose population level was estimated from reconstruction based on recovery of dead animals (1959-1982), on aerial surveys (1983-1993), and on simulations based on an empirical model of moose population rate of change (1994-2000). Population reconstruction was based on a field effort with an estimated recovery rate of 33%, employing corrections for seasonal bias in field effort, variable field effort, and moose yet alive. Wolf population level in 1959-1980 was best predicted ($r^2 = 0.84$) by density of old (>9 yr old) moose, which provide 67% of prey biomass for Isle Royale wolves, including a lag of 2 yrs for wolf response. Wolf numbers >1980 were lower than expected based on food abundance, which reached a low point in ca. 1990 and is predicted to rise rapidly during 1990-2000.

Key words: Canis lupus, moose, Alces alces, predation, population regulation

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The central role of food abundance has been emphasized in reviews of wolf population dynamics (Mech 1970, VanBallenberghe et al. 1975, Keith 1983, Peterson 1977, and Peterson and Page 1988). For top carnivores, population regulation by resource abundance ("bottom-up" control) is intuitively reasonable, and constitutes a basic tenet of ecological theory (Hairston et al. 1960, Fretwell 1987). Furthermore, on a regional scale, wolf density is positively correlated with ungulate density (Keith 1983, Fuller 1989), suggesting that an increase in wolf density will result from increased prey density. Yet long-term monitoring of wolf and moose populations at Isle Royale revealed opposing temporal trends in prey and predator density, interpreted as a lag in the predator population caused either by a decline in prey vigor as prey increased (Peterson et al. 1984a) or by changes in moose age structure (Peterson and Page 1988). Evidently a positive correlation between predator and prey at large spatial and temporal scales reveals little of the nature of wolf-prey interaction at the population level. Beyond its theoretical significance, a better understanding of proximal causes of wolf population change is obviously needed by managers who seek to balance human demands with the needs of native carnivores that rely on harvested prey populations (Gasaway et al., 1992).

Although Peterson and Page (1988:98) considered wolf food supply to be synonymous with the "abundance of moose in vulnerable age groups", their measure of wolf food supply was based on observed kill rates of wolves, not on an independent

measure of prey availability. In the present study we reexamined the relationship between food supply and density for Isle Royale wolves, estimating food availability for wolves by the abundance of old moose, the component of the prey population most significant to wolves.

STUDY AREA AND METHODS

Isle Royale National Park comprises a 544-km² island in Lake Superior, located 25 km from mainland Ontario. The island is covered by a mix of northern hardwood and coniferous forest, and is managed as a roadless wilderness national park. The island is open for recreational visitors only in non-winter months, when human activity is largely restricted to an extensive network of hiking trails. No mammalian pets are allowed on the island.

Isle Royale wolves feed almost entirely on moose in winter, and in summer, when beaver occur frequently in wolf feces, moose still provided an estimated 83% of ingested prey biomass in 1975-1983 (Peterson and Page 1988).

Wolves in Isle Royale National Park were counted from aircraft in Jan-Feb each year during 1959-1993. Results through 1986 were reported elsewhere (Mech 1966, Jordan et al. 1967, Wolfe and Allen 1973, Peterson 1977, and Peterson and Page 1988). The remaining years (1987-1993) are covered in Chap. 9.

Temporal changes in moose population size and age structure were determined by a combination of aerial census, simulation, and population reconstruction, or virtual population analysis

(McCullough et al. 1990, Fryxell 1988). In the latter approach, recoveries of dead animals were used to reconstruct a chronology of moose population parameters. Moose carcasses and skeletal remains were located during aerial and ground surveys each year, 1958-1991. Aerial surveys (85-185 hr) were flown annually for 50 consecutive days, weather permitting, beginning in late January. Flight lines covered the entire island, and an effort was made to locate all moose carcasses by following wolf and fox (Vulpes vulpes) tracks in snow. A constant annual effort was ensured by similar flight pattern and schedule, with only 2 pilots responsible for flying all surveys over a period of 33 years.

Ground surveys in summer, together with reports from park staff and visitors, provided an additional annual sample of dead moose. Year of death, if <2 years elapsed before discovery of the dead moose, was determined from the degree of decomposition of flesh and hair (presence of hide on bones indicated death within 1 yr, and all hair and remaining ligaments on bones disappeared after 2 yrs). Off-trail transects in a haphazard pattern provided most records of moose mortality from ground surveys. Calves less than 6 months old were excluded from analyses because of the high rate of disappearance of their fragile bones.

Three known sampling biases were rectified by adding a correction allowance to underrepresented groups in the raw data in proportion to the age distribution of dead moose in the corresponding year. First, the winter collections from non-calf

females were higher than for males (83mm:100ff, $N = 829$), but total skeletal collections from both winter and summer revealed a sex ratio that was almost equal (103mm:100ff, $N = 1,146$), as did aerial surveys of sex ratio (Peterson 1977 and unpubl. data). As a remedy, the non-calf male sample was expanded each year until a sex ratio of 103mm:100ff was attained for the total collection. No data was available on calf sex ratio or sex differences in calf survival, as feeding wolves destroyed most evidence of sex for moose calves.

Second, the number of moose recoveries each year during summer ground surveys was proportional to effort, expressed as the distance traveled off-trail ($r^2 = 0.59$, $F = 30.15$, 20 d.f., $P < 0.0001$). As a correction, the number of summer recoveries was adjusted each year to reflect a constant annual effort corresponding to median distance traveled off-trail (430 km).

Third, additions were made to recent cohorts in which animals remained alive. After the age of 9 yrs, when mean survival for non-calf moose was 0.63 for moose that had all attained the age of 1 yr, senescence-related mortality proceeded at a predictable rate, allowing a correction for moose still alive for cohorts born before 1982.

The combined recoveries from winter and summer field surveys, after correction for known biases, provided an annual sample of moose mortality that was used to "reconstruct" the living population over time. Age for each moose was determined by tooth eruption (if <16 mo. old) or counts of cementum

annulations (Wolfe 1969). On this basis each recovered moose with a known year of death was registered to an annual cohort, and the minimum number alive (MNA) each year was assumed to be a constant proportion of the total population that year. This proportion was estimated by comparison with aerial censuses of moose in winter (Peterson and Page 1993).

The reconstructed population analysis extended from 1959 to 1982. In order to continue an assessment of moose age structure during 1983-1993, an empirical model of moose population dynamics was constructed, and calibrated to the results of the reconstruction. The model incorporated as age-specific survival for each cohort a 5-yr running average of survival schedules for individual cohorts born in 1959-1982. Age-specific reproduction (the number of surviving 6-mo.-old calves per female) was adjusted until the model mimicked population history from 1959 to 1982, as revealed by reconstruction. The model was also used to evaluate the validity of reproduction and calf survival estimates, as field surveys of calf proportion were available for most years. Simulations using a range of previous fecundity and survival schedules were run to estimate population structure in the 1980s and 1990s, constrained by results of field surveys of calf abundance and population size.

A stochastic model was used to predict a range of moose population trajectories during 1994-2000, with 95% confidence interval. The basic population growth function used in the model was $N_t = N_{t-1} + (N_{t-1} * (r))$, where r = moose population finite

growth rate, N = moose population size, and t = year. " r " was assumed to be a random variable, normally-distributed variable with mean and variance defined by empirical values for r determined from annual aerial censuses during 1982-1993. The model was run 1000 times and the mean population size with 95% confidence interval was calculated for each year during 1994-2000.

RESULTS

Long-term collections of moose killed by wolves at Isle Royale confirmed the highly selective nature of wolf predation (Fig. 1), as revealed earlier (Mech 1966, Peterson 1977). Wolves exhibited strong selection for moose either < 1 yr old or > 9 yr old. Those > 9 yr old constituted 51% of all wolf-kills and 67% of ingested moose prey biomass, using estimated consumable prey weights provided by Peterson (1977). Moose > 9 yr old were thus considered to be the age group most indicative of actual prey availability for Isle Royale wolves.

Field surveys in 1958-1991 provided records on 1,001 dead moose > 6 mo old that could be placed into annual cohorts from 1958 to 1981. A correction for variable summer effort resulted in a mean adjustment of 0.026 and correction for sex bias bias resulted in a mean expansion of 0.103 for each non-calf male collected. Age-specific mortality (q_x) and survival (l_x) series were calculated for 524 moose > 1 yr old from the complete cohorts in 1958-1970. The composite l_x series was used to estimate the number of moose probably still alive in 1991 from

cohorts born in 1971-1982, resulting in the addition of 79 moose to the raw data.

After all corrections were applied, sample size was 1,071 moose, corresponding to a mean annual cohort sample of 43 moose. Additionally, 170 moose born before 1958 that were recovered during the study were included in the analysis as members of the post-1958 reconstructed population.

There was substantial variation in age-specific survival when cohorts were pooled at 5-yr intervals (Fig. 2), arising primarily from fluctuations in first-year survival. For 6-mo-old calves, survival through winter ranged from 90% (1963-1967) to 50% (1973-1977). After the age of 9 yr, senescence-related mortality increased steadily in all cohorts at a relatively constant rate.

The annual MNA increased from a low in 1958-1959 (190 moose) to a maximum in 1973-1974 (511 moose) before declining through 1982-1983 (Table 1). The ratio of MNA to total population size was estimated using 3 aerial censuses judged to be the most accurate of 14 conducted during 1960-1983. These estimates, 600 moose in 1960 (Mech 1966), $1,533 \pm 353$ moose in 1969 (Peterson 1977), and 984 ± 236 in 1979, assumed the proportion detected in census efforts was 83% for the total count in 1960 (Mech 1966) and 75% for the stratified sampling in 1969 and 1979 (Peterson and Page 1993). These census estimates were 2.9, 3.5, and 2.7 times greater than the respective MNA (mean = 3.0), thus total population size each year was estimated to be 3 times the MNA

from population reconstruction. Comparison to 11 other estimates from aerial censuses in 1965-1983, considered less accurate, indicated that $3 \times \text{MNA}$ was within the census 95% confidence interval (CI) in 7 years, higher than the census estimates plus CI in 3 yrs, and lower than the census estimate minus CI in 1 yr.

Based on reconstruction, Isle Royale moose increased slowly from 600 in 1959 to 800 in 1966, then doubled (to 1,600 moose) by 1972 (Fig. 3). A decline after 1974 brought the population down to 900 by 1983. Aerial census indicated that the decline was reversed in 1982, on the strength of a large cohort born in 1981 (Peterson and Page 1983), and that moose generally increased in the 1980s and early 1990s (Fig. 3). Simulations provided projections of moose population size and abundance of old moose through 1993, constrained by results of aerial censuses of moose.

Population projections were extended to the year 2000 using long-term average levels for survival and reproduction, similar to levels used to simulate population changes in the late 1980s. On this basis moose were projected to increase through the 1980s and 1990s, but projected abundance of old moose declined in the 1980s to a minimum in 1990 before increasing steadily in the 1990s. Population reconstruction, tied more directly to recoveries of dead moose, indicated that density of old moose reached a minimum in 1990-1992 before increasing.

During 1959-1979 wolf density was well-correlated with the abundance of moose > 9 yr old ($r^2 = 80\%$). Results from 1981-1982

were excluded from this comparison because disease possibly confounded wolf population dynamics during a population crash in that period (Chap. 9). Incorporating a lag for wolf response (1 yr, $r^2 = 81\%$; 2 yrs, $r^2 = 84\%$; 3 yrs, $r^2 = 74\%$) yielded the highest correlation for a lag of 2 yrs ($P = 0.0001$, $F = 102.85$).

In 1981-1982 the wolf population crashed dramatically (Peterson and Page 1988), then recovered briefly before declining to a minimum of 12 in 1988, the lowest level since the population was founded in the late 1940s. Expected wolf population level, based on the previous correlation with old moose, was to reach a maximum of almost 60 wolves in 1983 before declining to about 24 wolves by 1990. Observed wolf numbers diverged sharply from expectations in 1981-1982, then remained lower-than-expected through 1993 (Fig. 3).

DISCUSSION

The validity of this study rests completely on the accuracy of the moose population reconstruction. Population reconstruction has been used to assemble a population history for harvested populations of moose (Fryxell 1990) and black-tailed deer (McCullough et al. 1990), where long-term records on hunter effort and age-specific harvest were available. A high recovery rate (i.e. high harvest rate) is important when using mortality data from harvest, to eliminate natural mortality as a confounding factor (Roseberry and Wolff 1991).

In contrast, in this study the estimated recovery rate was approximately 33%, but all mortality was natural. Sampling

effort for dead moose in midwinter was consistently distributed over a 50-day period each year, and corrections for variable effort in ground surveys and sex bias in winter collections were introduced. We are aware of no additional biases that would significantly skew the results of the reconstruction. The population chronology produced by reconstruction may be smoothed slightly by errors in age determination, especially likely for old animals (Gasaway et al. 1978). Probably counteracting this effect is an increase in annual variability introduced by failure to accurately account for interannual variability in true age-specific survivorship (LaPointe et al. 1992).

Reconstruction provided a different and, we argue, more accurate chronology of moose population change than reported earlier (Peterson 1977, Peterson et al. 1984, Peterson and Page 1988), primarily in the timing and extent of the moose population decline in the 1970s. During that decade aerial censuses of the moose population were conducted only in 1972, 1974, and 1979, and previous annual estimates of moose population size were based largely on 2 indirect indices, the number of moose observed/100 km in summer ground transects, and the number of moose observed/hr during winter flights. The former index is subject to many potential biases, such as seasonal distribution of effort (Stephens 1981), and probably spatial distribution of ground coverage, observer experience and behavior, and prevailing temperature (Ackerman 1987), most of which remain unevaluated. The latter index is greatly affected by seasonal timing of

observations and habitat selection (Peterson and Page 1993).

Perhaps the weakest feature of the reconstruction is the calibration of the resulting population trend by selected aerial censuses. The 1960 total count was chosen as 1 of 3 used in the calibration because moose were unusually visible in deciduous forests that predominated in a burn dating from 1936 (Mech 1966). A major shift in winter distribution of moose toward coniferous cover was evident by the late 1960s, when census efforts were based on a stratified sampling of small plots counted by intensive search. The 1969 census was considered the best of the intensive search counts flown up to that time (Peterson 1977). Accuracy was variable for subsequent aerial censuses, all conducted by the senior author, but the 1979 count was considered among the most successful because of unusually favorable counting conditions. The spacing of selected counts at decadal intervals maximized the temporal span for calibration.

Recruitment of calves in the 1981 cohort was approximately double that of previous years, and subsequent aerial counts suggested that the moose population rate of increase was positive although relatively low until 1985. Population modeling revealed that even if age-specific survival and reproduction were constant, rate of population growth would remain low until the mid-1980s, when the number of reproducing moose increased. Thereafter population rate-of-increase would be positive and relatively high, subject to decline only when survival rate declined. The abundance of old moose would thereby begin

increasing in the early 1990s, providing wolves with favorable conditions for population growth.

We found that from 1959-1980 most of the variability in wolf density on Isle Royale could be explained simply by the number of old moose, their primary source of food. The abrupt population crash of 1981-1982 was a clear break with previous trends, and the continuing shortfall in wolf density in the 1980s, relative to their food supply, suggests that other factors, probably introduced disease, began to influence wolf numbers (see Chap. 9). Failure of Isle Royale wolves to increase in the 1990s, in the face of a steadily increasing food supply, will be the clearest indication that this population is no longer regulated by food resources (Fig. 4).

The major implication of this study, that prey age structure is more relevant than prey density as a determinant of wolf density, should be evaluated for other populations. Major fluctuations in age structure can occur in long-lived ungulates, and these may influence the degree of natural predation. The Isle Royale moose population probably contains a larger proportion of older, highly vulnerable prey than moose populations that are harvested. Yet wolves supported by moose consistently select old moose (Peterson et al. 1984b), suggesting that the majority of a moose population is unavailable as wolf prey. Whether or not wolf populations are generally influenced by prey age structure is especially pertinent for wildlife managers interested in evaluating wolf predation in

multi-predator systems which include humans as consumers. For example, does the presence of old moose buffer predation on moose calves in winter? What are the implications of harvest, especially any-sex harvest, on moose population age structure? Age structure of a moose populations is an important consideration in evaluating its vulnerability to predation as well as its intrinsic growth rate.

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Table 1. Relative population size for Isle Royale moose, indicated by the minimum number alive (MNA), calculated from recoveries of dead moose.

Total population			Total population		
Year	MNA	estimate	Year	MNA	estimate
1959	190	570	1971	484	1,452
1960	204	612	1972	507	1,521
1961	212	636	1973	500	1,500
1962	218	654	1974	511	1,533
1963	226	678	1975	480	1,440
1964	241	723	1976	453	1,359
1965	248	744	1977	399	1,197
1966	260	780	1978	350	1,050
1967	313	939	1979	359	1,077
1968	357	1,071	1980	327	981
1969	435	1,305	1981	308	924
1970	441	1,323	1982	293	879

FIGURE CAPTIONS

Fig. 1. Wolves prey on a select portion of the moose population. The long-term living age distribution for moose represents a composite survivorship series for cohorts born from 1958 to 1977 ($n = 866$), while the wolf-killed sample includes all known and probably wolf-killed moose with a known year of death, 1959-1982 ($n = 754$). Data for calves (< 1 yr old) was restricted to those between 6 and 12 mo old.

Fig. 2. Age-specific survivorship for moose, Isle Royale National Park, 1958-1981.

Fig. 3. (a) Long-term fluctuations in moose density are followed by similar changes in the number of old moose after a lag of almost a decade. Simulations of moose population dynamics were adjusted to mimic results for the reconstructed population in 1959-1981 and aerial censuses during 1982-1993 (top), then simulation was used to provide an estimate of abundance of moose > 9 yr old (bottom). (b) For 1994-2000, moose population projection with 95% confidence interval is based on a stochastic model using observed population rate of growth in 1980-1993.

Fig. 4. Estimates of abundance for moose > 9 yr old coincide closely for reconstruction and simulation (top). In 1959-1980 observed wolf population size correlated well with predictions based on abundance of moose > 9 yr old 2 years earlier, then fell below expected levels in 1981-1993.

Selectivity of Wolf Predation

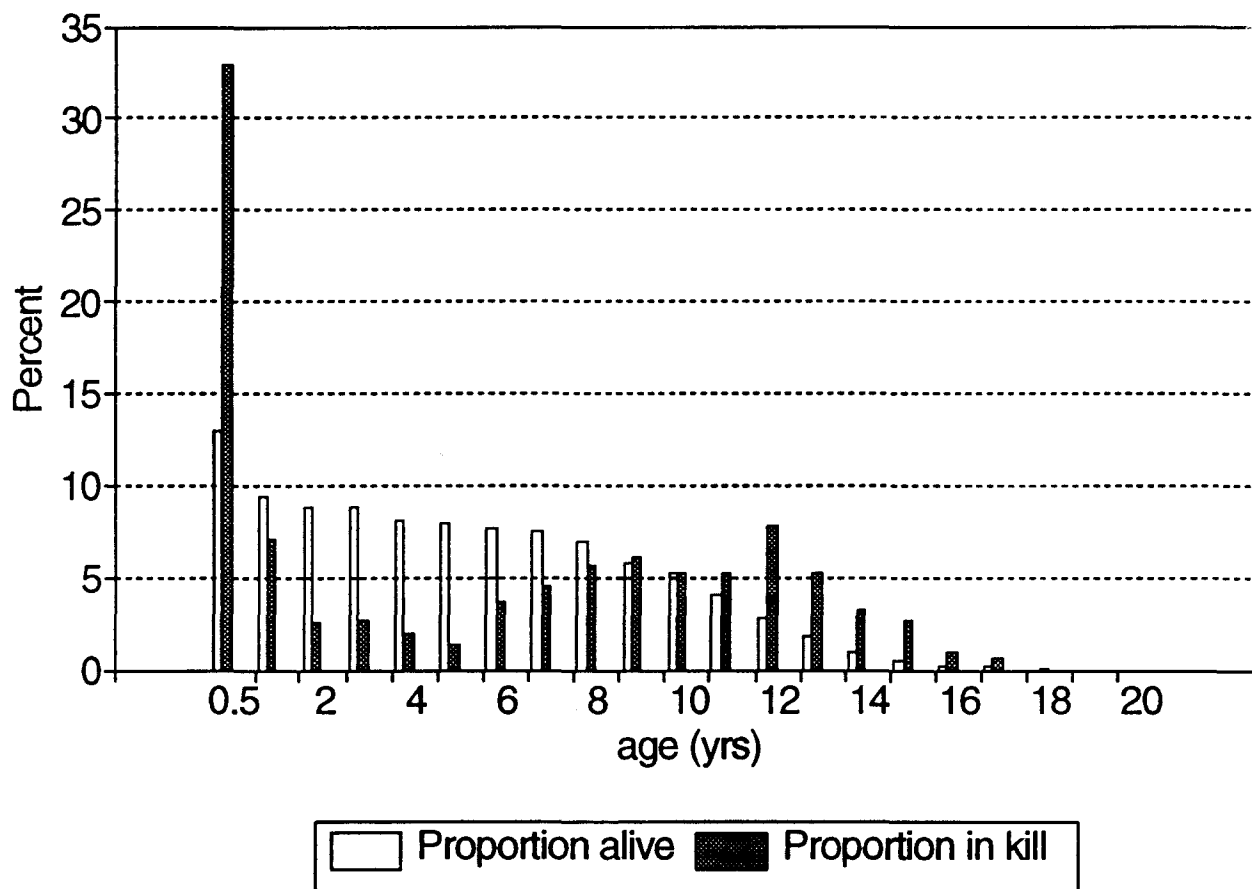


Fig. 1

Moose Survival, 5-yr Intervals (by year of birth)

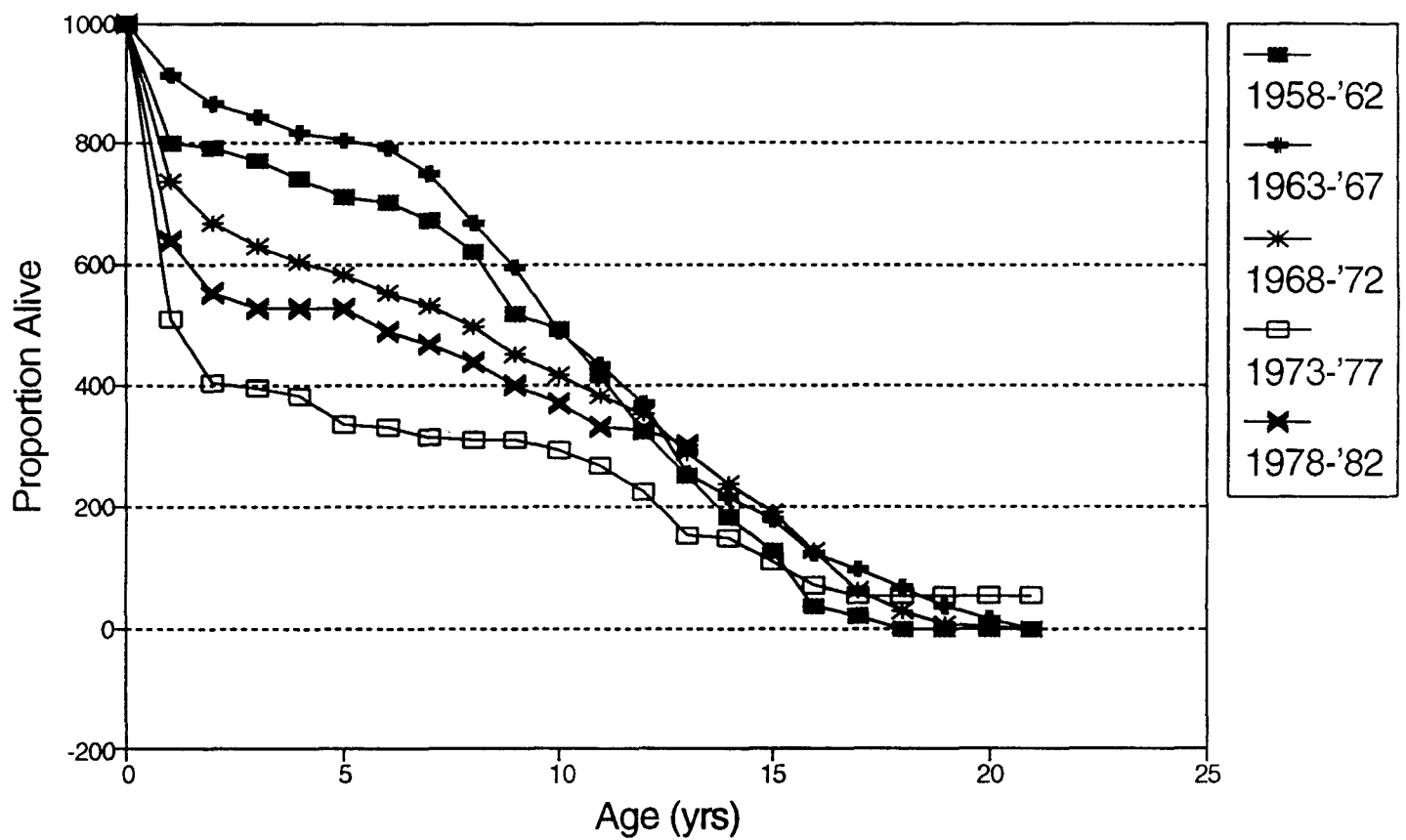
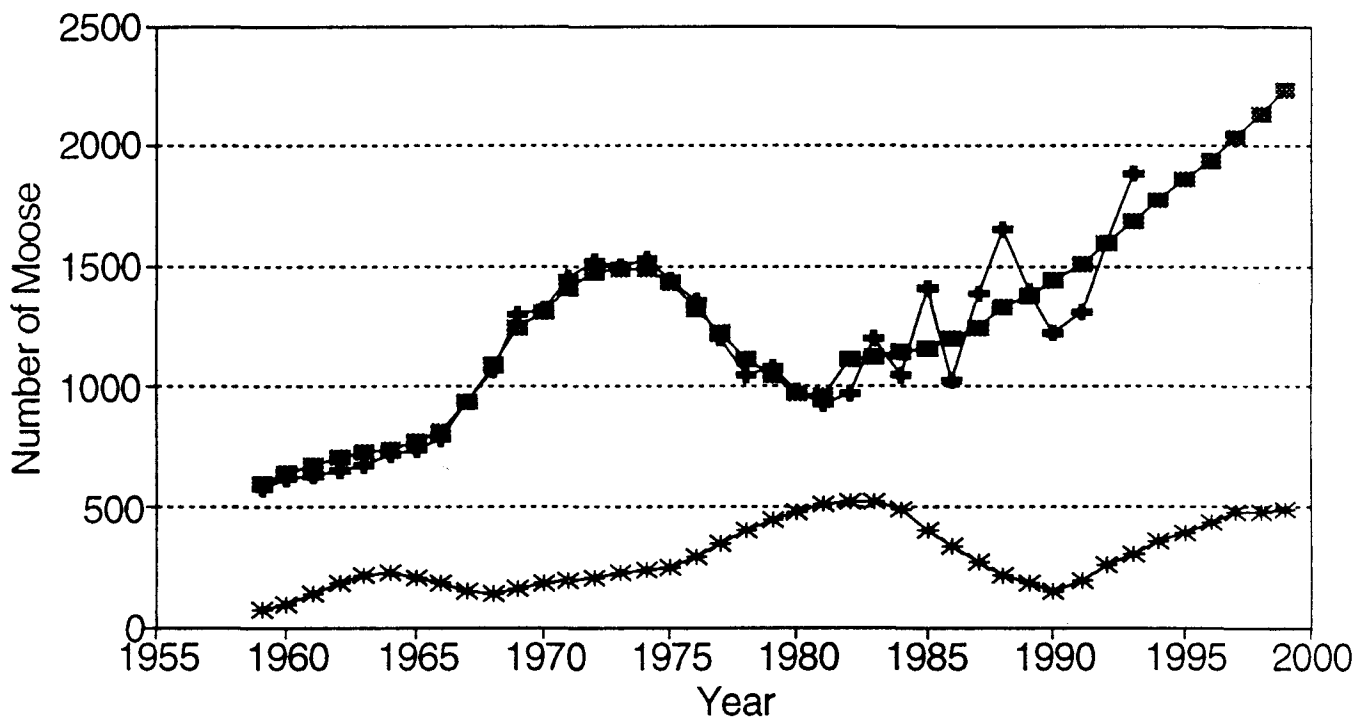


Fig. 2

Moose Population Trajectory (with # of moose >9 yr old)



—■— Total moose, simul. —+— # moose, recon+count —*— # moose >9 yr old

Fig. 3a

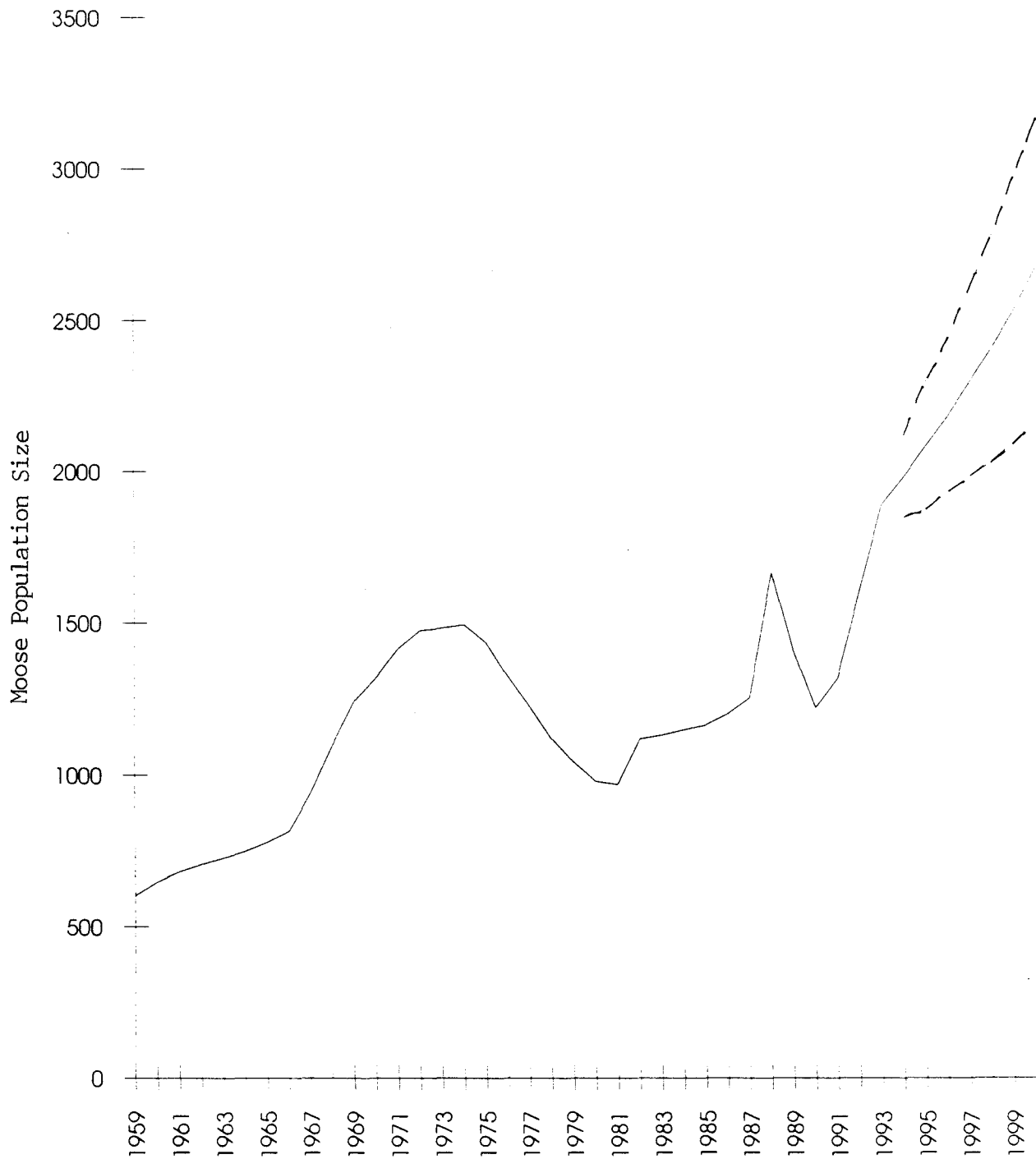


Fig. 3b

Wolf nos. & old moose

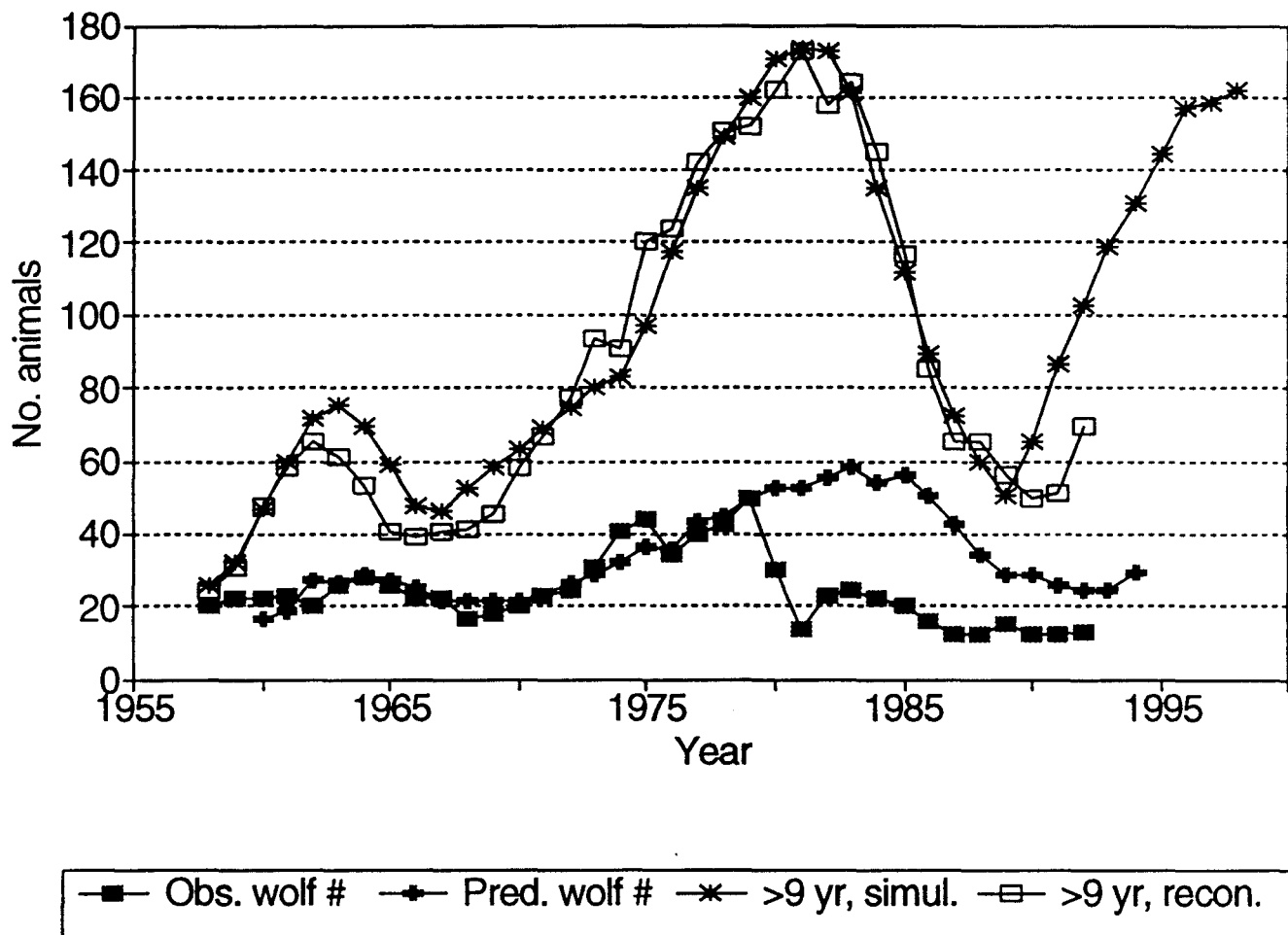


Fig. 4