MOOSE ON KALGIN ISLAND: ARE DENSITY-DEPENDENT PROCESSES RELATED TO HARVEST?

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ABSTRACT: We studied the demography of a population of Alaskan moose (*Alces alces gigas*) that was closed to immigration or emigration on Kalgin Island, Alaska, USA, from 1980 to 1987. This island population experienced neither severe weather nor predation from large mammalian carnivores. Effort and success by hunters was monitored carefully, and the age structure from harvested moose was used to estimate population size during each year. Moose were harvested heavily during permit hunts to reduce the population that had overshot carrying capacity. The estimated population declined from 212 to 8 moose between 1982 and 1986. Harvest was linearly related to population size, but moose killed per unit of hunter effort (CPUE) exhibited a disparate pattern with hunter success initially declining with population size but then increasing dramatically at lower population sizes of moose. The overall age structure of moose became younger as harvest reduced the size of the population. The percentage of moose 3.5 - 5.5, and 6.5 - 12.5 years old declined with population size, whereas 0.5 year-old moose increased as the population declined. Recruitment of yearlings into the population on Kalgin Island exhibited a strong density-dependent response. Our analysis indicated an extremely high intrinsic rate of increase ($r = 0.35 - 0.44$) for those moose. Even with that high productivity, moose on Kalgin Island could not withstand the heavy harvest to which they were subjected, which exceeded maximum sustained yield during the early years to meet initial management objectives. Moose on Kalgin Island exhibited a strong density-dependent response to harvest, and we hypothesize that density-dependent mechanisms interact with harvest, predation, and severe weather to influence other populations of moose in Alaska.

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Regulation of populations of large mammals is thought to involve strong density-dependent mechanisms, especially among the Cervidae (Klein 1968, 1981; McCullough 1979; Clutton-Brock *et al.* 1982; Skogland 1985; Boyce 1989). This paradigm likewise has been forwarded to explain the population dynamics of moose (*Alces alces*) (Bowyer *et al.* 1997, Van Ballenberghe and Ballard 1998). Nonetheless, controversy and debate over the mechanisms that limit and regulate populations of moose continue (Van Ballenberghe and Ballard 1998), in part, because of the confounding effects of predation and severe weather (Gasaway *et al.* 1983, 1992; Messier 1994; Van Ballenberghe and Ballard 1994), and interactions among predation, weather, and density dependence (Bowyer *et al.* 1998, 1999a). Sorting among these potential mechanisms for understanding regulation of moose populations is important because some authors have suggested that northern populations of ungulates may not exhibit density dependence (Bergerud *et al.* 1983a, b; Gasaway *et al.* 1983; Bergerud 1992; Boertje *et al.* 1996).

We recognized that a retrospective

analysis of data on Alaskan moose (*A. a. gigas*) collected by one of us (JBF) offered a unique opportunity to test hypotheses related to a density-dependent response to harvest in a population closed to immigration and emigration that had experienced mild winters and no predation. We tested whether hunter effort and harvest varied inversely with population size of moose, whether recruitment rate of moose declined with increasing population size, and whether the age structure of moose became younger as harvest increased. All those outcomes would be expected from a density-dependent response by moose to a decline in population size from harvest. Finally, we discuss outcomes from our study in light of historical and existing paradigms for the management of moose in Alaska, and of northern ungulates in general.

STUDY AREA

We studied the population dynamics of moose on Kalgin Island, which is located in Cook Inlet, Alaska, USA (60°27'N, 152°00'W). The island encompasses about 60 km^2 and is characterized by stands of white spruce (*Picea glauca*) with an alder (*Alnus* spp.) understorey, interspersed with muskeg bogs; there are several fresh-water ponds and a small inlet. Kalgin Island is about 8 km from Redoubt Point and 23 km from the Kenai Peninsula (the nearest weather station); the island is accessible only by boat or small plane with floats, and there are no roads on the island. The swift and treacherous tidal currents in Cook Inlet have prevented the natural colonization of Kalgin Island by large mammals.

The climate of Kalgin Island is maritime with cooler temperatures and less snowfall than inland areas at similar latitudes. Precipitation averaged 62 cm at the nearby Kenai Weather Station; summer temperatures averaged 12°C and winter temperatures averaged -3°C. Snowfall was highly variable and reached a maximum of 71 cm during our study.

Moose initially were introduced to Kalgin Island in 1957; by 1959, 3 young females and 3 young males had been translocated to the island (Burris and McKnight 1973). The absence of wolves (*Canis lupus*) and bears (*Ursus* spp.) coupled with a mild climate allowed the rapid growth of the moose population. By 1970, the moose population on Kalgin Island attracted the attention of local hunters, and the first hunting season was opened in the autumn of that year. The moose population continued to grow over the next decade, and had reached a very high density by the early 1980's. Because the population was at high density and ostensibly had exceeded carrying capacity (*K*) of the island, the Alaska Department of Fish and Game intentionally initiated a heavy harvest, and then attempted to maintain a density of about 1 moose/2.6 km^2 through harvest permits that allowed the taking of any sex or age class of moose. The moose population declined markedly from that harvest and reached very low numbers by 1986-1987. That variation in population size and the harvest of animals of known sex and age from 1981 to 1987 allowed us to investigate the dynamics of a population of moose in an environment lacking predators or severe winters, and without the confounding effects of immigration or emigration.

METHODS

Data on hunter effort and success were gathered from 1981 to 1987 by the Alaska Department of Fish and Game through a mandatory program that required permit holders to supply information about their hunt on Kalgin Island. Noncompliant hunters were further encouraged with the use of court orders to provide the requisite information. Ultimately, >99% compliance was achieved, yielding a data set on hunter effort and success that was both comprehensive and complete.

Each moose removed from Kalgin Island was sexed and the front teeth of the lower jaw were collected from hunters. Age of individual moose was determined by grinding the incisors and reading cementum lines in those teeth (Sergeant and Pimlott 1959, Gasaway *et al.* 1978). The difficulty and expense of reaching the island made a large number of illegal kills unlikely. Data on sex and age of moose were used for population reconstructions and for assessing changes in sex and age structure of the population over time.

Aerial surveys of Kalgin Island also were conducted in early winter following the hunting season with a small fixed-wing aircraft except during 1984. The sex of moose was determined through the presence of antlers in males or a white vulval patch on females (Mitchell 1970, Roussel 1975, Bowyer *et al.* 1991). We categorized individuals as adult males, adult females, and young of either sex. Unfortunately, the intensity of aerial surveys and patterns of searching for moose varied from year to year and were not quantified consistently. Moreover, no correction for sightability was performed (*sensu* Gasaway *et al.* 1985, Peterson and Page 1993, Timmerman 1993, Lenarz 1998). Consequently, we used data collected via aerial surveys to determine which sex and age classes of moose to include in our recruitment models; no estimations of population size were attempted with those data.

We obtained climatic data from the Kenai Weather Station, which of nearby stations provided data most similar to those for Kalgin Island. Although conditions likely were more moderate on Kalgin Island than on the Kenai Peninsula because of the maritime climate of the island, the Kenai Weather Station provided a reliable index to general patterns of climatic variability for the region. Snow conditions, especially depth, are thought to be crucial in the productivity of moose populations, in particular the survivorship of young (Coady 1974, Rolley and Keith 1980, Peterson *et al.* 1982), whereas temperatures in winter are thought to be far less important (Bowyer *et al.* 1997). Thus, we evaluated total snowfall, snow depth (accumulated through winter), and maximum depth of snow in relation to the demographics of the moose population.

Populations of moose were reconstructed from hunter harvests using the conventional method of accumulating cohorts derived from harvests (Hesselton *et al.* 1965, Lowe 1969, McCullough 1979). We recognize that this method assumes equal catchability, which is likely to be violated by selectivity of hunters, and that survivorship and fecundity are fixed (Eberhardt 1985). We controlled for the latter two assumptions by only reconstructing the population within years. Statistical analyses of population demographics were accomplished via simple linear regression, including comparisons of slopes, or Spearman rank correlations (r_s) where assumptions of parametric regression could not be met, as were analyses between population variables and climatic values (Zar 1984). In addition, we further evaluated the recruitment rate of yearlings against population size using principal-axis regression (Sokal and Rohlf 1969) to control for a potential lack of independence in those variables. We used piece-wise regression for evaluating data related to catch per unit effort (Neter *et al.* 1985). We estimated the maximum intrinsic rate of increase (r_{max}) and carrying capacity (K) using regression (McCullough 1979) and calculated the intrinsic rate of increase (r) and finite growth rate (λ) achieved by the population over time using the equations presented by Van Ballenburghe and Ballard (1998).

Following McCullough (1979), we used

the number of adult females as the most appropriate parameter of population size with which to assess density-dependent effects on recruitment; primarily adult females compete with one another and young for resources thereby influencing their physical condition and ultimately rates of recruitment. Adult males and females spatially segregate from one another for most of the year among polygynous species of ruminants (Bowyer 1984, Bleich *et al.* 1997), and sexual segregation can occur on a fine scale provided a heterogeneous environment is available (Bowyer *et al.* 1996). Sexual segregation has been well-documented in moose (Miquelle *et al.* 1992), and the sexes use and select habitats differentially outside the mating season (Miller and Litvaitis 1992, Miquelle *et al.* 1992); such selection by females may occur on an exceptionally fine scale (Bowyer *et al.* 1999b). We also present a population model with both sexes combined so that we can use the full data set on age structure. We adjusted *K* to true *K* to compensate for the absence of natural mortality in our model (McCullough 1979) and because we believed the population reconstructions overestimated recruitment at *K*. The magnitude of the reduction in *K* is similar to that proposed by McCullough (i.e., 22%), but we acknowledge this value is somewhat arbitrary.

RESULTS

Population Size

Population reconstructions based on hunter kills from 1981 to 1987 indicated moose on Kalgin Island were most abundant in 1982 and least so in 1986 (Fig. 1); a total of 252 moose were harvested over the 7 years of this study. The rate of decline from peak to low numbers of moose was extreme when determined from population reconstructions (r = -0.819, λ = 0.441). Population density based on reconstructions indicated there were about 3.5 moose/km^2 in 1982 and 0.1 moose/km^2 in 1986.

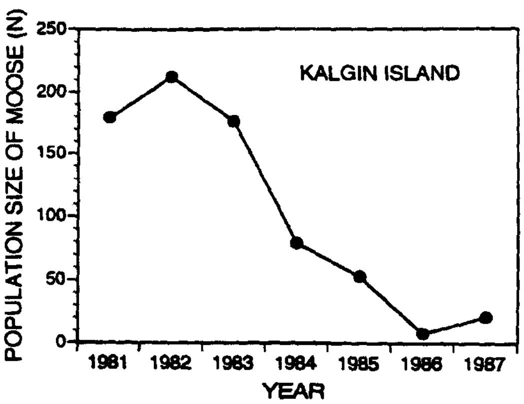

Fig. 1. Estimated population size (N) of Alaskan moose on Kalgin Island, Cook Inlet, Alaska, USA, from 1981 to 1987. Population sizes were estimated annually from reconstructions based on age structure of harvested moose.

Hunter Effort, Success, and Selectivity

Effort expended by hunters to harvest moose was large, especially in 1982 when >700 hunter days were recorded. A positive relation existed between the population size of moose and the total effort expended in an attempt to harvest one; the greatest departure from linearity occurred in 1985 when effort remained high while the population size of moose declined precipitously (Fig. 2).

The number of moose harvested was strongly and linearly correlated with the size of the moose population on Kalgin Island (Fig. 3). Success of hunters (moose killed/hunter day), however, showed an unexpected pattern. As predicted, hunter success initially declined as the size of the moose population was reduced. At lower population sizes of moose, however, the success of hunters rose unexpectedly (Fig. 4). Piece-wise regression indicated a cut point for those disparate trends at a population of about 75 moose or a density of 1.2 animals/km^2 (Fig. 4).

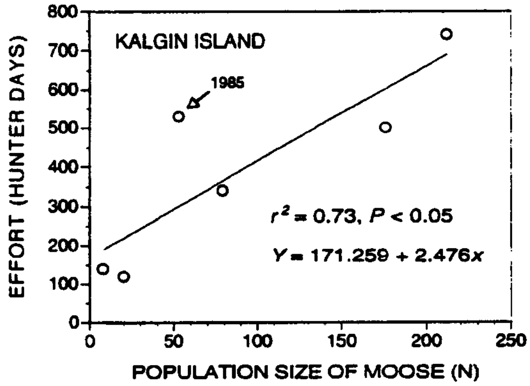

Fig. 2. Relation between hunter effort and estimated population size of moose on Kalgin Island, Cook Inlet, Alaska, USA, 1981-1987. Note the high effort relative to population size in 1985.

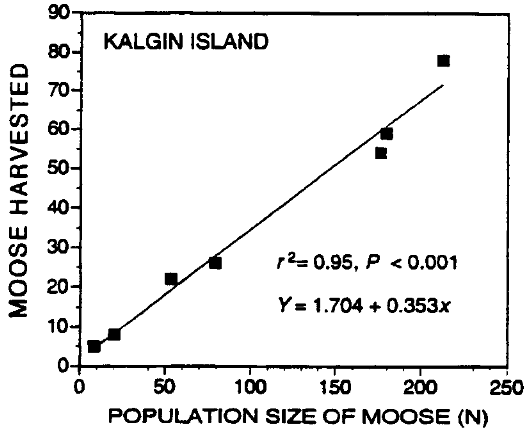

Fig. 3. Relation between number of moose harvested and their estimated population size on Kalgin Island, Cook Inlet, USA, 1981-1987. Despite the large amount of variance explained in harvest by population size, harvest alone should not be used as an index to population size.

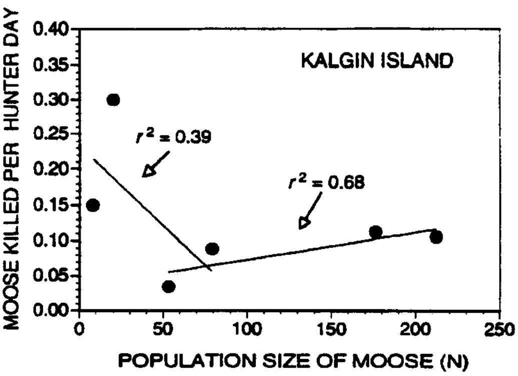

Fig. 4. Catch per unit effort (moose killed per hunter day) in relation to estimated population size on Kalgin Island, Cook Inlet, Alaska, USA, 1981-1987. Piece-wise regression indicated a change in direction for this relationship at a population size of about 75 moose.

Based on differences in the percentage of sex and age classes in the harvest and those observed in aerial surveys, hunters selected adult males (16 ± 13.4% SD), but avoided killing young (-9 ± 8.8% SD) and adult females (-8 ± 9.2% SD). The average ratio from data on harvest indicated 105 adult males:100 adult females, whereas aerial surveys yielded 38 adult males:100 adult females. The sex ratio of young (0.5 years old) in the harvest approached parity (110 males:100 females) and exhibited no obvious trend with population size.

Sex and Age Structure of Moose

Young, yearlings, and 2-year-olds predominated in the harvest and always composed >50% of the kill (Fig 5). Moose 6.5-12.5 years old slowly disappeared in the harvest from 1981 to 1987, although small sample sizes may have contributed to that outcome in 1986-1987. Indeed, the general

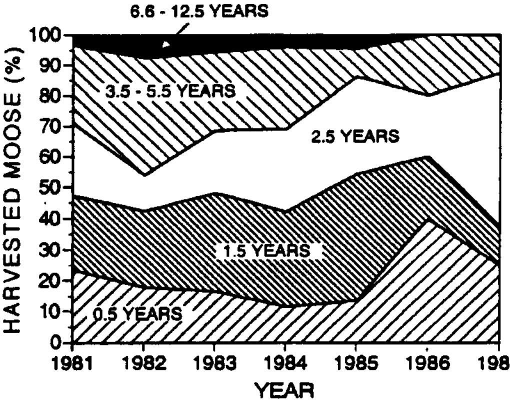

Fig. 5. Age structure of moose harvested on Kalgin Island, Cook Inlet, Alaska, USA, 1981-1987. Note the decline in older age classes through time.

pattern was for young (0.5 years) to increase proportionally and older age classes to decline with decreasing population size (Fig. 6). The overall result was a strong positive relation between population size and the mean age of moose (Fig. 7). This same pattern held when we restricted our analysis to only adult females ($\bar{X}$=3.1 years old). Mean age of females increased significantly with population size ($P < 0.05$); at low population density there were few females >5.5 years old.

Effects of Winter Snowfall

Snowfall, which ranged between 10-71 cm during our study, was unrelated to the population dynamics of moose on Kalgin Island. Snow depth, which ranged from 3 to 29 cm, was unrelated to population size ($r^2 = 0.09$, $P > 0.5$) or the ratio of young:adult females ($r^2 = 0.04$, $P > 0.6$). An additional time lag failed to improve the regressions ($P > 0.6$). Finally, ratios of yearlings:adult or yearlings:adult female were unrelated to snowfall or snow depth with 1 or 2 year time lags ($r^2 \leq 0.1$, $P > 0.4$ for all regressions).

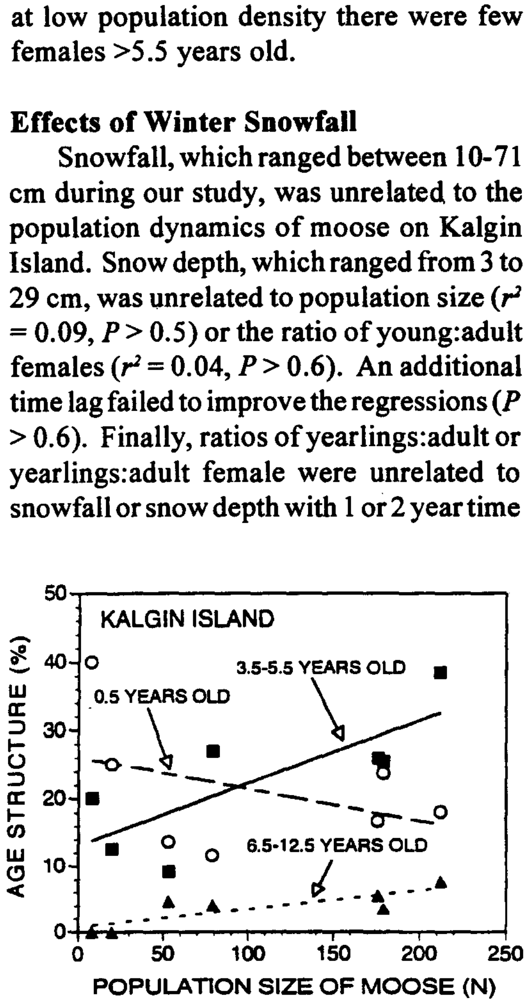

Fig. 6. Changes in age structure of moose with increasing population size, Kalgin Island, Cook Inlet, Alaska, USA, 1981-1987. Open circles = 0.5 years old, closed squares = 3.5 – 5.5 years old, and closed triangles = 6.5 – 12.5 years old. Note the increase in older age classes and decline of young moose with increasing population size.

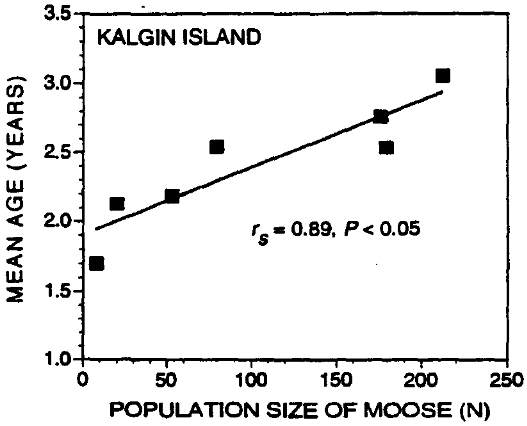

Fig. 7. Mean age of moose in relation to population size, Kalgin Island, Cook Inlet, Alaska, USA, 1981-1987.

Modeling the Moose Population

We used our population reconstructions to model the dynamics of moose on Kalgin Island. We recognized that young likely were underrepresented in our reconstructions because hunters killed them less often than their proportional occurrence in the population. Consequently, we selected yearlings (1.5 years old) as our most unbiased estimate of recruitment. In addition, we evaluated survivorship of cohorts estimated from our population reconstructions during those years and for those age classes for which we had sufficient data. Although survivorship was low and moose died young (Fig. 8) because of the heavy harvest (Fig. 3), our population reconstructions were not biased by changing survivorship among cohorts, at least from 1981 to 1984 (Fig. 8); slopes of regressions did not differ ($P > 0.37$).

We observed a strong, negative relation between the rate at which yearlings were recruited and the size of the moose population (Fig. 9). Principal-axis regression indicated that 98% of the variation in recruitment rate was explained by population size, with the effects of population size in calcu-

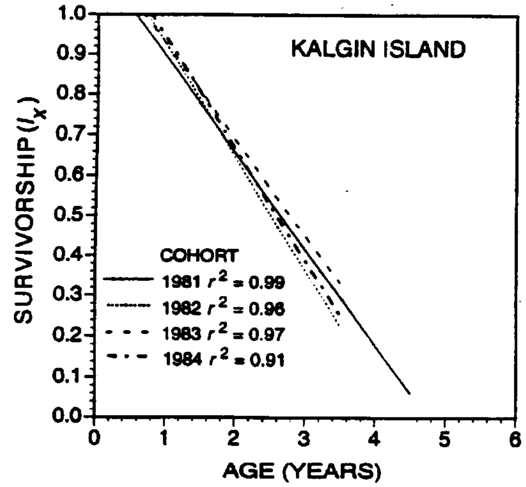

Fig. 8. Survivorship (l_x) of moose estimated from the age structure in the harvest, Kalgin Island, Cook Inlet, Alaska, USA, 1981-1984. Note the similarity in survivorship among cohorts.

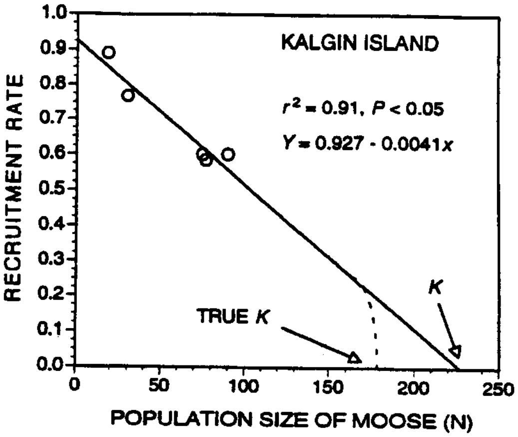

Fig. 9. Relation between recruitment rate (yearlings/adult) and population size of moose on Kalgin Island, Cook Inlet, Alaska, USA, 1981-1987. Carrying capacity (K) is estimated from regression, but "true K" reflects the tendency for regression to overestimate that parameter.

lating the dependent variable (yearlings/adult) controlled. Thus, this relationship infers density dependence and is not caused by a lack of independence between the axes of the regression. Of necessity, the regression model (Fig. 9) extrapolates well beyond data used to construct this relationship at high density, because recruits (yearlings) represent a large proportion of the total population, and young (0.5 years old) are not included. A regression approach to estimating K is known to overestimate that parameter; in this instance $K = 225$ moose (Fig. 9). Our highest estimate from population reconstructions was 212 animals, which likely represented an overshoot of K. Consequently, we expected K to be much lower and have assigned a "true K" of about 175 animals.

We also constructed this same model using adult females as the independent variable. The same strong inverse relation was obtained ($r^2 = 0.83$, $P > 0.05$; $Y = 0.913 - 0.0056x$). In this model, K was estimated at 165 adult females, and true K probably was about 128 animals. The model with both adult males and females as the independent variable did not have a significantly different intercept on the Y-axis ($P > 0.2$) or significantly improve the fit over that of the model for females alone ($P > 0.5$), although r^2 was about 10% higher with the sexes combined (Fig. 9).

Both models indicated an exceptionally high rate of recruitment for moose, and if the value for adult females is adopted, $r_{max} = 0.913$ (i.e., from the Y-intercept of the regression line predicting recruitment rate from population size). For both models, data used to calculate r_{max} lie close to the Y-axis, and extrapolations to at least $K/2$ (estimated from regressions) are mathematically and biologically reliable.

Although r_{max} can be calculated from regression, this value assumes no adult mortality. Moreover, standard methods for calculating r require that density-dependent effects be included across periods of population growth (i.e., growth is S-shaped). Thus, for comparative purposes we modeled the growth of moose using the parameters from Fig. 10. By starting with 10 moose and allowing unimpeded growth for 8 years, the population reached 225 moose (the regression estimate for K). The intrinsic rate of increase for this population was $r = 0.39 = (\ln 225 - \ln 10)/8$. If, however, 175 moose are assumed to be true K, the population overshoots K in year 7 (from 156 moose in year 6), and attains a population size of 219 moose, and $r = 0.44$. Similar results are obtained from the linear regression equation for female moose ($Y = 0.913 - 0.0056x$). Ten moose reach a population size of 163 females (near the regression estimate of $K = 165$) in 8 years, yielding $r = 0.35$. If true K is assumed to be about 128 females, the population overshoots slightly in year 6 and produces $r = 0.43$.

We also assessed the maximum sustained yield (MSY) for this population of moose from a recruitment parabola (Fig. 10). We again show the model combining adult males and adult females, principally because we have arranged most data in that fashion. MSY would be achieved at an adult population size of 113 moose and total potential harvest of 52 animals. That point would occur at 50% of K estimated from regression (e.g., the relationship is linear), 53% if the highest population reconstruction (e.g., 212 moose) is used, and 65% of K if our guess for true K (e.g., 175 moose) is employed. A similar model for adult females can be constructed from the regression equation for recruitment rate, and yields MSY = 38 moose for an adult population size of 83 adults.

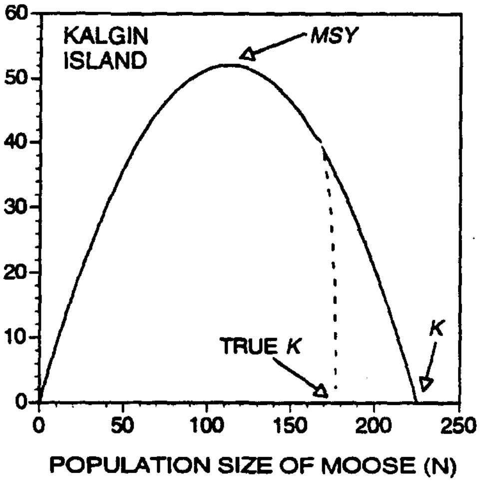

Fig. 10. Recruitment number (yearlings) in relation to population size of moose, Kalgin Island, Cook Inlet, Alaska, USA, 1981-1987. The parabola is calculated from the regression line in Fig. 9. MSY (Maximum Sustained Yield) occurs at the peak of the parabola.

If the actual harvest of moose (Fig. 5) is compared with the population model (Fig. 10), the response of the population can be estimated. The outcome, of course, depends upon the starting value for K; starting with 225 moose is most conservative. In this instance, however, the solution is academic: 3 years of harvest exceed MSY, and the remainder of years is higher than, or at what the population can sustain for those particular population sizes (i.e., harvest lies on or above the recruitment parabola). As initially intended, the harvest markedly reduced the size of the population, but was too high to maintain a density of 1 moose/2.6 km^2 (Fig. 3). A near-identical result is obtained by examining harvest of adult females relative to their recruitment parabola (i.e., MSY = 38 moose): the harvest is sufficient to drive the population toward extirpation.

DISCUSSION

Advantages and Biases of the Data Set

The moose population on Kalgin Island offered a unique opportunity to test hypotheses concerning the dynamics of a hunted population while engaging in adaptive management (Romesburg 1981, McNab 1983). The population was likely closed to immigration and emigration, although we have no data on moose that may have drowned attempting to emigrate. The remote location and special means needed to travel to the island made illegal kills unlikely. Effects of severe winters on population processes were negligible because of the mild maritime climate. Populations of moose are known to be affected adversely by deep snow (Coady 1974, Rolley and Keith 1980, Peterson *et al.* 1982, Mech *et al.* 1987, Van Ballenberghe and Ballard 1998), but snow depths on the island were well below minimum levels thought to hinder movements of moose (60-70 cm). Snow characteristics were uncorrelated with the demographics of this population of moose. No wolves or bears occurred on Kalgin Island and losses to predators were nonexistent. Such losses can have profound effects on population dynamics of moose elsewhere (Ballard *et al.* 1991, Gasaway *et al.* 1992, Van Ballenberghe and Ballard 1994, Bowyer *et al.* 1998). Moreover, the moose population on Kalgin Island was driven from high to low density over 7 years and the sex and age composition of the harvest were known. Detailed information on hunter effort and success were obtained from nearly everyone who hunted.

Although data collected from Kalgin Island are unique for assessing the effects of hunting on dynamics of a harvested moose population, several assumptions of those analyses have the potential to bias some results. We did not account for the kill that likely occurred from crippling of moose by hunters, which may have been as high as 15% of the harvest (Gasaway *et al.* 1983); this omission makes our estimates of mortality of moose from hunting conservative. In addition, population reconstructions that make inference about recruitment require the assumption of a stable age distribution because fecundity and survivorship are fixed. That assumption is unlikely to be met in a population that is rapidly undergoing change; data on age structure (Fig. 5) indicated that assumption was violated. We minimized that bias by reconstructing the population each year. We also determined that survivorship of various cohorts did not vary through time (Fig. 8). Moreover, by considering all moose $\geq$2.5 years as adults in our population model, we lessened the effects of changes in adult age structure on our predictions. The direction and magnitude of any remaining bias, however, is somewhat uncertain. Nonetheless, we hypothesize that the nature of the bias in our data is to overestimate recruitment at K. That outcome seems likely because the standing age distribution at K (or especially in an overshoot of K) would include animals that were recruited when the population was still increasing. Consequently, when we accumulated cohorts to reconstruct the population (*sensu* McCullough 1979), those moose that were recruited when the population was still growing rapidly would lead us to overestimate recruitment at K. Unfortunately, we have no way to test this hypothesis, because we do not know how rapidly the population approached K. If our assumption is correct, however, the primary effect would be to reduce the slope (i.e., adjust it toward zero) of the regression line between recruitment rate and population size (Fig. 9); hence, the need to reduce K to true K. Effects on the Y intercept, and thereby our estimates of r_{max} would be far less pronounced because of the close proximity of our data to the Y axis (Fig. 9).

Hunter Effort and Success

Potential biases notwithstanding, data on the behavior of hunters on Kalgin Island provide important insights into using hunter success or catch per unit effort (CPUE) as an index for assessing trends in population size. The positive relation between population size and harvest was strong and linear (Fig. 3). That outcome was obtained, however, by a more variable (but still significant) correlation between hunter effort and population size (Fig. 2). Effort during 1985 was especially high relative to the size of the population (N = 53), ostensibly because hunters had been successful in previous years. We do not recommend using kill as an index to population size despite the high correlation between those variables because of the potentially confounding effects of effort. Hunter success (moose killed per hunter day; Fig. 4) or CPUE has been suggested as an index to population size (Hatter 1998). Fryxell *et al.* (1988) cautioned that departures from linearity between population size and CPUE might occur at high effort because of interference among hunters, a pattern not evident in our data (Fig. 4). Indeed, the patterns we observed were far more pernicious. Hunter success initially declined with population size in a classical density-dependent manner (*sensu* Crête *et al.* 1981) to about 75 moose, but then increased at a high rate (Fig. 4). We hypothesize that the increase occurred because those individuals hunting when moose were at low density were a highly skillful subset of those hunting when moose were plentiful. Whatever the cause, data presented in Fig. 4 emphasize that hunter success should not be used as an index to population size. Caughley (1974) demonstrated that sex and age ratios should not be used to assess trends in populations without an independent measure of population size. We make that same suggestion for CPUE.

The Recruitment Model

The inverse relation between recruitment rate of yearlings and the size of the population infers a strong density-dependent response to harvest (Fig. 9). Although we did not add stochasticity to our model, our deterministic approach is sufficient to test for density dependence in recruitment, especially since we controlled for a potential lack of independence between the dependent and independent variable with principal-axis regression. We chose yearlings as the most reliable estimate of recruitment from our standing age distributions; young often are underestimated by such analyses because they are under-represented in the kill (McCullough 1979, Boer 1988). Age distributions we used for reconstructions assumed a stable-age distribution, which was not met. Our data, however, are not biased by variable survivorship among cohorts (Fig. 8), although we have too few years of data for a complete cohort analysis (Fryxell *et al.* 1988, Ferguson 1993). Survivorship of moose on Kalgin Island show a linear pattern typical of heavily harvested populations (Boer 1988), with truncation in older age classes (Fig. 6) compared with unhunted populations (Peterson 1977).

Although the relationships in Figs. 5, 6, and 7 were predicted from hypotheses concerning density-dependent processes in populations of moose, the age structure we obtained yielded a young population, especially at high density. Moose on Kalgin Island were thought to have exceeded carrying capacity (*K*) at high density (1980-1982) because of the extensive barking of trees, browsing of alders and white spruce, and eating of roots observed during summer and autumn of those years. Indeed, a comparison of incisor wear by moose on Kalgin Island with moose harvested in Game Management Units 14 and 16 (on either side of Cook Inlet) indicated that by 8 years old, moose on Kalgin Island had patterns of wear typical of 16-year-olds on the other units. Thus, extreme wearing of teeth at high density likely resulted in a young age structure for moose inhabiting Kalgin Island when the population was near or beyond *K*. Heavy wear of teeth has been reported in overshoots of *K* for another cervid (Skogland 1984).

Recruitment models (*sensu* McCullough 1979) have several advantages over more traditional approaches. Most importantly, they allow an assessment of the role of density dependence on recruitment by combining the effects of age structure, survivorship, and fecundity for a particular population size. Moreover, population models that do not incorporate density dependence often conclude that population growth is most sensitive to survivorship of adult females (see Van Ballenberghe and Ballard 1998 for a review); a result that can be circular and trivial. If fecundity is fixed by age class and cannot vary with population size, then only survivorship of adults can change the trajectory of the population. Incorporating stochastic variation does not alter this conclusion; far less variability typically can be assigned to fecundity compared with values for survivorship of a particular age class. Moreover, survivorship and fecundity both co-vary with population size, and separating those variables can lead to misconceptions about how populations are regulated. For instance, populations held at low density by predation (Gasaway *et al.* 1992, Van Ballenberghe and Ballard 1994, Bowyer *et al.* 1998) are influenced principally by survivorship of young, not adults.

The regression approach also allows estimation of r_{max} and K without making the assumption of fixed schedules of survivorship and fecundity inherent to life tables (Caughley 1977), although K likely is overestimated by the regression method (McCullough 1979). Our analysis allowed a precise estimation of r_{max} (Fig. 9), even though this value was surprisingly high. Empirical methods of estimating r by examining changes in numbers over time led Keith (1983) to conclude that the largest values of r ranged from 0.14 to 0.26 for moose. Van Ballenberghe (1983) considered $r = 0.35$ might be the maximum moose could attain under natural conditions, although Cederlund and Sand (1991) reported a higher value ($r = 0.40$) for moose not subjected to heavy predation, and speculated that $r = 0.47$ might be possible. Depending upon the model used (with and without adult males) and whether K or true K was employed, we obtained values of r between 0.35 – 0.44. These values are especially sensitive to the number of years over which the calculation is made, because density-dependent processes slow growth of the population as it approaches K. Nevertheless, we believe our calculations bracket what might be possible for moose under conditions of mild winters, no predators, and no immigration or emigration. We do not believe our estimates of recruitment were biased by hunter selectivity because we used yearlings as recruits, and adult females were only slightly underrepresented in the kill. McCullough (1979) likewise extended what was thought to be the maximum reproductive rate for white-tailed deer (*Odocoileus virginianus*) by collecting data under similar circumstances. Reproductive rates of moose can be quite high (twinning rates of 32-64%) even in areas of interior Alaska where winters are severe, providing that populations are held at low density relative to K (Bowyer *et al.* 1998). We hypothesize that areas with a mild climate and no predation allow rates of population increase for moose that are higher than previously recognized. Both high twinning rates by adults and reproduction by yearlings would be necessary to explain the high rate of productivity on Kalgin Island; indeed, twinning rates and pregnancy among yearlings are positively correlated in moose (Boer 1992). The high rate of increase for moose on Kalgin Island leads us to hypothesize that emigration, losses to predation or effects of severe winters may be greater than previously thought in other areas of Alaska.

MANAGEMENT IMPLICATIONS

The density that moose reached on Kalgin Island was high (3.5/km^2) relative to other reports from the literature. For large areas in interior Alaska and the Yukon, Gasaway *et al.* (1992) reported that moose populations subjected to heavy predation ranged in crude density from 0.05 to 0.4 moose/km^2; populations where predation was not thought to be limiting ranged from 0.2 to 1.4 moose/km^2. Ballard *et al.* (1991) noted that the population density of moose across Alaska ranged from 0.05 to 1.2 animals/km^2. Low-density populations of moose, however, can have localized areas, such as rutting grounds, where density can be high (Molvar *et al.* 1993). Van Ballenberghe and Ballard (1998) emphasized that local densities of 5 moose/km^2 were possible, and irrupting populations might temporarily exceed 2.5 moose/ km^2; those populations, however, are unlikely to sustain such high densities over long periods (Gasaway *et al.* 1992). Nonetheless, high population density can occur for short periods on habitats of comparatively low quality where large overshoots of *K* occur (McCullough 1979). Indeed, density can be a misleading indicator of habitat quality (Van Horne 1983). We believe that the high density of moose attained on Kalgin Island (3.5/ km^2) resulted from such an overshoot of *K* (because of excessive toothwear in older age classes), and because moose would have difficulty emigrating from the island. Deterioration of habitat and associated nutritional problems are a well-documented consequence of overpopulation in northern cervids (Klein 1981). Such density-dependent effects are moderated mostly via nutrition (Simkin 1974; Saether and Haagerud 1983,1985; Schwartz and Hundertmark 1993).

Variability in density of moose caused by differences in quality of habitat, rates of predation, or intensity of harvest make direct comparisons of density among populations problematical (Weixelman *et al.* 1998). The relationship of the population to *K*, whether influenced by harvest, predation, or climate, is the primary factor influencing recruitment (Fig. 10). Consequently, populations at identical densities but with different *K*'s would exhibit different rates of recruitment. This potential outcome is why population density measured independent of some index to *K* should not be used to determine the status of a population or its allowable harvest.

Recruitment rates of yearlings into the moose population on Kalgin Island were dependent upon the number of adult moose (Figs. 9 and 10). Estimates of r_{max} were similar, however, whether we use just adult females or combined the sexes in those calculations. That outcome likely occurred because the sexes of cervids spatially segregate from one another, and use habitat differently, for much of the year (McCullough 1979, Bowyer 1984, Miller and Litvaitis 1992, Miquelle *et al.* 1992). Even when populations reach high density and spatial overlap between the sexes increases, males and females still may avoid competition by partitioning of the dietary niche (Kie and Bowyer 1999). Consequently, adult males compete less intensively for resources with females and young than do other females (McCullough 1979, Bowyer *et al.* 1997). Thus, a harvest of adult males will have less effect on recruitment and population growth than will killing females (McCullough 1979).

Our results indicate that strong density-dependent processes occurred in moose on Kalgin Island subjected to harvest (Fig. 9), and offer support for the conceptual model provided by Van Ballenberghe and Ballard (1998) for population dynamics of moose. Indeed, short of a manipulative experiment involving controls and treatments, which would be difficult to perform with moose at a sufficiently large scale, our data are among the strongest evidence for density dependence in moose.

Density dependence should be viewed as a life-history characteristic of a species (Stearns 1977, 1992; Stubbs 1977; Pianka 1983), and an important component in the population dynamics of most large mammals (McCullough 1979, Clutton-Brock *et al.* 1982, Skogland 1985, Fowler 1987, Boyce 1989). Such density-dependent processes underpin the dynamics of moose populations and other large herbivores, and we suggest effects of climatic severity, predation, and harvest need to be considered in conjunction with density dependence. The failure to detect density-dependent mechanisms among ungulates likely stems from invalid comparisons of density made across populations, not comparing adequate changes in density within a population, and from confounding effects of climate, predation, harvest, and genetics (McCullough 1979, 1990; Cederlund *et al.* 1991; Sand 1996; Saether 1997; Coulson *et al.* 1998; Post and Stenseth 1998). Indeed, even strong correlations between population parameters and climatic variables often are mediated by density dependence among large herbivores (Bowyer *et al.* 1988, 1999a). Our point is that if severe winter conditions, predation, or harvest fail to regulate populations of moose, then density-dependent mechanisms will do so. Moreover, such density-dependent processes often will interact with other variables (such as climate and predation) to determine recruitment rates and other parameters of moose populations.

Some populations of northern cervids were thought to seldom experience density-dependent properties, or if they did so, that such effects were unrelated to nutrition (Bergerud *et al.* 1983a, b; Bergerud 1992). Indeed, populations of moose in interior Alaska were not thought to exhibit strong density-dependent characteristics (Gasaway *et al.* 1983, Boertje *et al.* 1996). This assessment, however, cannot be made based only on density, harvest, or changes in population size; it requires information on the relationship of population size to *K*. For example, this same conclusion could be reached for moose on Kalgin Island (i.e., the moose population did not rebound from harvest), yet those moose exhibited strong density dependence. We do not suggest that moose on Kalgin Island were mismanaged; the initial objective of markedly reducing their numbers was met. Moreover, assigning blame for past overharvest of moose in interior Alaska discussed by Gasaway *et al.* (1983) is not our purpose; modern management would likely prevent the types of problems documented by Van Ballenberghe (1985). Our point is that management of moose on Kalgin Island resulted in a harvest that could not be compensated for by recruitment even in a highly productive population of moose exhibiting a strong density-dependent response because the kill was too high. Yet, our results clearly indicate that moose on Kalgin Island exhibited a strong density-dependent response to harvest. We hypothesize that overharvest, coupled with predation and severe weather, also was a contributing factor for other populations of Alaskan ungulates failing to respond in the expected density-dependent manner (Boertje *et al.* 1996). We believe that the role of density dependence in the management of Alaskan ungulates needs further consideration, and how density dependence, severe weather, predation, and harvest interact to influence the dynamics of moose populations needs further study.

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