POPULATION DYNAMICS AND LIFE HISTORY TRADE-OFFS OF MOOSE (*ALCES ALCES*) IN SOUTH-CENTRAL ALASKA

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Abstract. A common framework toward understanding the ecological forces affecting herbivore population dynamics is to partition those forces according to their origin higher ("top-down") or lower ("bottom-up") on the trophic chain. I employed that framework to describe phenotypic life history trade-offs in a large herbivore, moose (*Alces alces*). The relative importance of top-down and bottom-up ecological constraints to female moose in south-central Alaska was appraised at the population level by analyzing population size, growth, and winter habitat of moose, and the size and impact of their principal predator populations (wolves [*Canis lupus*] and brown bears [*Ursus arctos*]). At the individual level, longitudinal mortality and reproductive patterns of radio-collared individuals were studied to estimate vital rates and life history trade-offs that could be attributed to nutrition and predation, respectively. The population was essentially stable through the 1980s and early 1990s, and began declining in the period of this study (1994–2000). Nutritional constraints on productivity were evident in low twinning rates (9–24%) and delayed age of first reproduction (3.4 yr) relative to other moose populations. However, the decline of the population was due principally to high rates of summer mortality of calves, resulting in low recruitment in the fall (0.11–0.22 offspring/female) and increasing adult mortality. Bear and wolf densities were high and moderate, respectively, while human harvest of moose was limited to males. Modeled population growth indicated a very limited capacity for population recovery through increased reproduction when compared to the effects of reducing predation. Constraints on population growth were mirrored in life history trade-offs. Trade-offs that were attributed to bottom-up effects included reduced rates of both parturition and twinning as a consequence of maternal investment in the prior year. Important trade-offs also were detected between top-down factors and reproductive effort through significantly increased predation on adult females with calves and increased survival of yearlings when adults skipped or abandoned reproductive attempts and extended the duration of maternal care.

Key words: Alces alces; *brown bears; browse; Cervidae; cost of reproduction; models; moose; Nelchina; population dynamics; predator–prey; ungulates; wolves.*

INTRODUCTION

In North America, a large body of evidence points to widespread limitation of moose (*Alces alces* L.) populations by natural predators, primarily wolves (*Canis lupus* L.), brown bears (*Ursus arctos* L.), and black bears (*Ursus americanus* Pallas; Van Ballenberghe and Ballard 1994, Ballard and Van Ballenberghe 1998, Hayes et al. 2003). Evidence for nutritional limitation is less common, but well supported in some cases (Peterson 1977, Messier 1991, Van Ballenberghe and Ballard 1994, Bowyer et al. 1999). In any given instance, wildlife ecologists usually must piece together a mélange of circumstantial evidence for what limits population growth, whether for theoretical, conservation, or consumptive purposes. Often overlooked in the search for such evidence are life history trade-offs that can be roughly divided by the same underlying trophic framework of "bottom-up" or "top-down" that is often applied to population limiting factors. Nutritional constraints for a population can be mirrored in greater expression of the life history trade-off between present and future reproduction by individuals (Clutton-Brock et al. 1987a, Testa and Adams 1998). In populations limited by predation, one might also expect to see top-down trade-offs in reproductive effort that affect survival of adults and other offspring. Not only might such trade-offs be indicative of the strength of population-level trophic interactions, but the interaction of life history trade-offs may alter expected population dynamics (Testa 1998, 2004).

The phenotypic life history trade-offs considered here are negative correlations that occur between an individual female's fecundity in successive years (bottom-up), and positive correlations between present reproduction by individual females (birth of offspring) and subsequent predation on adults or their previous offspring (top-down). These are a subset of possible

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life history trade-offs, or "costs of reproduction" (Stearns 1992). Here I assume that the primary effect of bottom-up, or nutritional factors is on reproduction, while top-down, or predation constraints act on survival, though I recognize that such causes may not be mutually exclusive. Poor nutrition might affect vulnerability to predation in a variety of ways (Peterson et al. 1984, Bartmann et al. 1992) or predation pressure may alter foraging behavior and affect nutrition (Lima and Dill 1990, Laundré et al. 2001). However, the study of such indirect interactions should follow the demonstration of more direct relationships of predation and nutrition to life history alternatives.

Both positive and negative correlations have been found between present and future fecundity of individuals, but the negative correlations expected from life history theory appear to be more likely where nutritional or other stress factors occur (Clutton-Brock et al. 1987a, Festa-Bianchet 1989, Stearns 1992). The most detailed studies of life history trade-offs in ungulates usually attribute their underlying mechanism to energetic, or "bottom-up," causes. This is reasonable in the near absence of predators and considering the obvious energetic and nutritional demands of reproduction (Albon et al. 1986, Clutton-Brock et al. 1989, Thomas 1990, Heard et al. 1997, Festa-Bianchet 1998, Testa and Adams 1998, Keech et al. 2000). Less obvious, and probably less common, is the relationship between nutritional constraints, accentuated by previous reproductive demands, and adult survival. Examples of increased adult mortality as a consequence of reproductive effort in mammals are few and usually come from populations with little or no risk of adult predation (e.g., Clutton-Brock et al. 1983).

That reproduction can include heightened risk of predation is implied by behavioral trade-offs between foraging and predator avoidance (Lima and Dill 1990, Berger 1991, Bleich et al. 1997, Kie 1999, White and Berger 2001). More explicit costs from predation that are imposed by reproduction are known in a variety of taxa (Magnhagen 1991), but there are few examples from the mammalian literature (Cushing 1985, Klemola et al. 1997). Such risks can only be expected where predators capable of killing adult animals are a significant component of the ecosystem, a condition for ungulates that has been eliminated with the large carnivores in broad areas of North America and Europe (Berger 1999).

Moose in the Nelchina Basin, south-central Alaska, provided an opportunity to observe the simultaneous effects of top-down and bottom-up ecological forces on both population dynamics and life history trade-offs. This population was maintained at fairly high density for ~25 years prior to this study (Ballard et al. 1991). From 1977 to 1984, moose twinning rates were in the middle of the range reported for other North American moose populations (Franzmann and Schwartz 1985, Ballard et al. 1991, Boer 1992, Gas-

away et al. 1992), but have declined in recent years (Testa and Adams 1998) indicating nutritional constraints on reproduction. Predation by bears and wolves in that period caused significant adult mortality and was especially heavy on calves (Ballard et al. 1991). This impact by predators occurred in spite of the seasonal presence of caribou (*Rangifer tarandus* L.), which serve as alternative prey for wolves and bears in the area.

My objective here is to compare the roles of top-down and bottom-up factors in limiting the population of moose in the Nelchina Basin, south-central Alaska, and in imposing life history trade-offs for individuals in that population. I address the question of whether bottom-up and top-down ecological constraints at the population level find similar expression in the life history trade-offs of individuals. This is done at the population level by analyzing population size, growth, and winter habitat of the moose population, the size and impact of their principal predator populations, and the potential for moose population growth under alternative assumptions about reproduction and survival. At the individual level, longitudinal mortality and reproductive patterns of radio-collared moose were studied to estimate vital rates and the magnitude of life history trade-offs that could be attributed to nutrition and predation, respectively. The interaction of top-down and bottom-up life history trade-offs at the level of the individual may influence the dynamics of the population beyond that expected from gross changes in age-specific survival and fecundity (Testa 1998). The population dynamic consequences of that interaction are explored through simulations in a companion report (Testa 2004) based on the results reported here.

STUDY AREA

Moose were studied in an area of ~4200 km² near the abandoned town site of Nelchina (62°6′ N, 147°10′ W) in south-central Alaska (Fig. 1). In defining the Nelchina Study Area (NSA), I included only elevations <1230 m as potential moose habitat. The Chugach and Talkeetna mountain ranges insulate the area from coastal influences on precipitation and temperatures. Annual temperatures range from −50° to 32°C with 22–42 cm of precipitation, mostly snow (Skoog 1968). The study area included subalpine heath and woody shrubs such as dwarf birch (*Betula nana* L.), speckled alder (*Alnus incana* [L.] Moench.), and willow (primarily *Salix pulchra* Cham., *S. alaxensis* [Anderss.] Coville, *S. glauca* L.) in foothills of the Talkeetna Mountains in the west, progressing to a boreal forest of mixed birch (*Betula papyrifera* Marsh), aspen–poplar (*Populus tremuloides* Michx. and *P. balsamifera* L.), and spruce (*Picea glauca* [Moench] Voss and *P. mariana* [P. Mill.] B.S.P.) in hills and lowlands to ~800 m elevation. Bogs of sphagnum, sedges, and low shrubs, with scattered *P. mariana* were extensive in lower areas, predominantly the east-
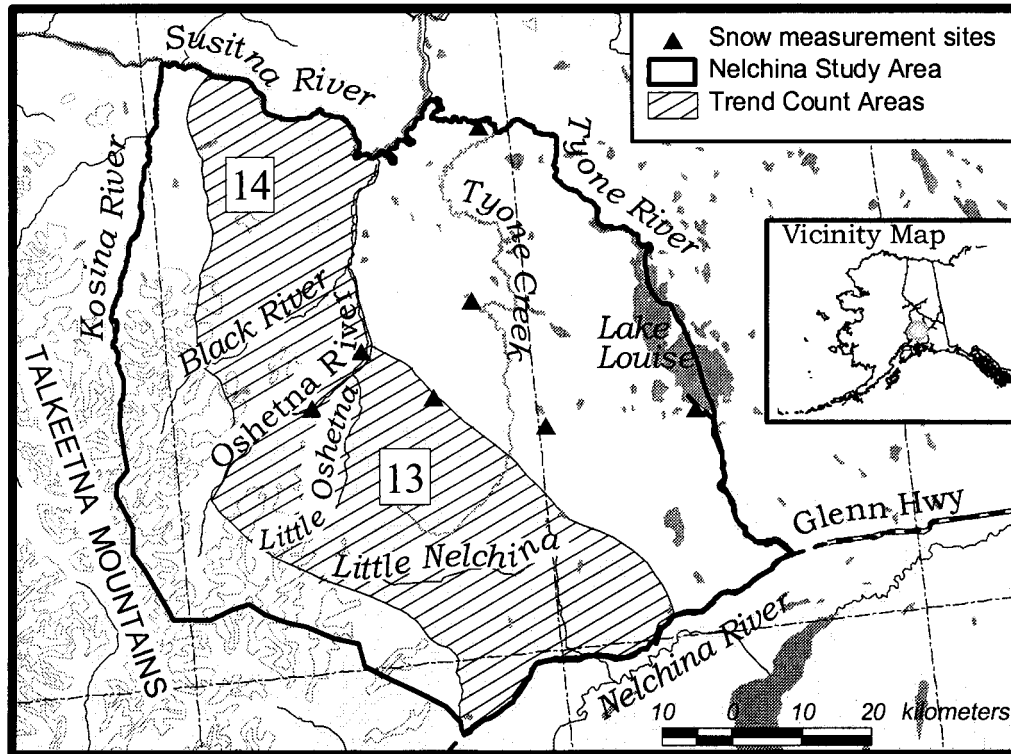
FIG. 1. The Nelchina Study Area in south-central Alaska, with traditionally surveyed moose Count Areas and snow measurement sites.

ern portion of the study area from 620 m to 800 m elevation.

Moose, caribou, wolves, and brown bears of the Nelchina Basin have been studied for over 40 years (Ballard et al. 1987, 1990, 1991, Miller et al. 1997). Moose breed polygynously in late September–early October and adult females give birth to one or two calves in late May–early June each year (Schwartz 1998, Testa 2002, Testa et al. 2000a, b). Calves that survive the summer wean in August, but will remain with their mother until the next calf is born the following spring (Schwartz 1998), or for an additional year if no new calf is born (personal observation). In a study area that encompassed my own, but was roughly four times larger, indices of moose density increased in the 1940s and 1950s, possibly as a result of federal wolf control, reaching a peak in 1963, and lower peaks in 1975 and the mid 1980s (Ballard et al. 1991). Estimates of moose density from various parts of the Ballard et al. (1991) study area from 1980 to 1985 ranged from 0.270 to 0.892 moose/km² and were in the upper 25% of densities reported from other areas of Alaska (Ballard et al. 1991). In the period of this study, the Nelchina caribou herd was present and could serve as alternative prey to wolves and bears in the NSA during the calving season (May–June), but dispersed over the remainder of Game Management Unit (GMU) 13 (~60 000 km²) in summer and was absent from October to April. The

herd declined from ~39 000 adults in spring 1995 to ~30 000 in 2000 (B. D. Scotton, personal communication).

METHODS

Population-level assessments

Composition and density of moose.—Moose were surveyed each fall from Piper PA/18 "Supercub" aircraft in two traditional Count Areas (CAs) of Game Management Unit (GMU) 13A (Fig. 1) at an intensity of 0.6–1.1 min/km², roughly half the intensity used for density estimation (Gasaway et al. 1986). Such surveys have been made to detect trends in the area since 1955 (Ballard et al. 1991), but only those after 1980 were analyzed for comparison to the period of this study, 1994–2000. The two CAs comprised 2000 km² of the 4200 km² in the Nelchina Study Area (NSA), including the areas of highest moose density.

Moose were identified in surveys as calves (<1 yr old), and males and females older than calves (Van Ballenberghe 1979). The sex of calves was not determined. Ratios of males to females and calves to females varied substantially from year to year due to varying harvest of males and annual changes in calf recruitment, respectively. Because these may obscure demographic trends and because female moose are the most important segment to population growth, numbers

of females/km^2 were emphasized in survey analyses. In 1994–1997 and 1999–2000 the number of radio-collared moose in the surveyed area was determined daily by radio tracking. The probability of sighting moose was then estimated from the proportion of radio-collared moose present that were seen during the survey, with variances and confidence intervals estimated by bootstrapping (Efron 1982).

Immediately following the CA surveys in 1994 and 1998–2000, estimates were made of the moose population in the NSA. In 1994 and 1998, sample units of ~40 km^2 were drawn on a map of the area, choosing boundaries that could be visually identified from the air. In 1994, low-intensity "stratification" counts made by observers in a Cessna 185 on one day were related by probability regression (Sarndal et al. 1992:219) to intensive counts (1.5–2.3 min/km^2) made by pilot/observer teams in PA/18 aircraft the following day. This regression was then used to estimate the number of moose in sample units that were not surveyed by the PA/18 crews (J. M. Ver Hoef, *personal communication*). Sightability correction factors (SCFs) were determined on the intensive sample units by resurveying a 2.6-km^2 subunit at 4–5 min/km^2 (Gasaway et al. 1986). In 1998 standard stratification and estimation methods (Gasaway et al. 1986) were used, including SCFs.

In 1999 and 2000, moose density was estimated by stratified block kriging (Ver Hoef 2001). The principal statistical innovation of this method is the incorporation of spatial autocorrelation in the estimates. Rectangular sample units (~16 km^2) defined by latitude and longitude were located with Global Positioning System (GPS) receivers. Stratification of the area was accomplished subjectively by low intensity surveys. Randomly selected units were flown at higher intensity (~2.5–4 min/km^2) than in a normal Gasaway survey, but SCFs were not applied. Bias relative to earlier methods was assumed to be small (<5%) because this search intensity approached that at which SCF plots were flown in earlier surveys and SCFs historically increased estimates by only ~11% (Gasaway et al. 1986; J. M. Ver Hoef, *personal communication*).

Snow depths.—Snow depths were measured in cooperation with the United States Natural Resources Conservation Service (NRCS) monthly from late January to late March. Based on Coady (1974), Ballard et al. (1991) considered a mean depth of 74 cm in this period as indicative of a "severe" winter that could reduce survival of moose. I measured snow depths in the same way from two sites (Square Lake and Lake Louise) within moose habitat (elevations <1230 m) from 1994 to 2000, and from five additional sites from 1995 to 2000.

Browsing intensity.—Willows (*Salix* sp.) are the most common forage detected in winter fecal samples from moose in the NSA (Testa, *unpublished data*). I estimated the relative intensity of winter browsing by moose by the percent *S. alexensis* stems that were browsed in riparian habitats along Tyone Creek and Oshetna River (Fig. 1), important wintering areas where *S. alexensis* is the most common willow species. Ten transects were selected in stands of *S. alexensis* at 1.6-km intervals along the stream in late winter (March) each year from 1995 to 2000. At 4-m intervals along each 100-m transect, the nearest aboveground plant of *S. alexensis* was selected and the browsed condition of the nearest twigs (growth from the previous summer) at 1 m and 2 m above ground level, plus the terminal shoot if ≥1 m and ≤3 m high were recorded. Densities of snowshoe hare (*Lepus americanus* Erxleben) were low, and tracks in snow supported the assumption that moose were the main source of *S. alexensis* browsing. Regression analysis was used to relate browsing of twigs to mean winter snow depths at the nearest snow measurement location.

Predator populations.—From 18 May to 1 June 1998, a Capture–Mark–Resight (CMR) technique was applied to brown bears in a 2150-km^2 portion of GMU 13A, principally the northern half of the NSA (Miller et al. 1997, Testa et al. 2000c). The study area for density estimation was chosen to contain representative habitats in the NSA and important concentrations of calving moose and caribou in the drainages of Tyone Creek and the Oshetna, Little Oshetna, and Black Rivers (Fig. 1). Bears with radio collars were located within the study area boundary on each day of the survey by observers using a radio receiver and a fixed-wing aircraft, while four pilot/observer teams in fixed-wing aircraft simultaneously searched the entire area to sight bears and determine which of those were radio collared. Analysis was performed with program NOREMARK (White 1996).

Wolf density estimates were made in March 1995, February 1996, and March 1997 using aerial tracking methods described by Becker et al. (1998). Wolves harvested before the surveys, as determined from mandatory reporting forms submitted by trappers and hunters, were added to the survey results to estimate minimum fall density of wolves. In 1998–2000 no formal estimates of wolf density were possible because snow conditions were inadequate for tracking. In those years, minimum estimates of wolf density were made by counting the number of unique packs (determined by location, color, and number of members) that were seen in the NSA during telemetry and survey flights from October to February.

Radio-collared moose

Capture and handling.—Female moose (≥2 years old) were captured and equipped with VHF radio collars in March, November, and December 1994, and November 1995 and 1997. Ten to 18 female calves (10–11 months old, "short yearlings") were captured, weighed, and equipped with expandable radio collars each April 1995–1997 and 1999. Except for 13 moose

that were captured by helicopter net/gun on 16–17 November 1994, all captures were made by darting from a helicopter with a mixture of carfentanil-citrate and xylazine hydrochloride (Schmitt and Dalton 1987).

Survival and reproduction.—Radio-collared moose were tracked by observers in fixed-wing aircraft at least once each month from January to November. From 1994 to 1998, parturition of radio-collared females and survival of their calves were monitored daily from mid May to mid June (weather permitting), every 2–3 days in late June, and biweekly in July (Testa et al. 2000a). In spring 1999 and 2000, we tracked each moose daily only until parturition or mid June, then resumed a monthly tracking schedule thereafter.

Only rarely was a moose that was being radio tracked not also seen from the air. The rate of sighting the females' calves exceeded 96%/day. Survival was estimated for the annual cycle (May–April) using the staggered entry design and comparisons were made with Z tests (Pollock et al. 1989) for calves (0–11 mo), female yearlings (12–23 mo), and adult females (≥24 mo). Moose were excluded from survival analyses for two weeks after their capture. Calves of radio-collared females were treated as if they were also radio-collared (Pollock et al. 1989). Missing calves were considered dead if they could not be found in three successive searches. When adult females that were accompanied by a calf died, that calf was assumed to have died at the same time. Cause of mortality was attributed to a predator if there was surface evidence of a chase or struggle, or if sightings were obtained daily and a predator was observed eating a moose that appeared healthy and active during the previous flight. Causes of calf mortality usually could not be determined. Tests related to predation were conducted by treating nonpredation deaths as censored data. Trend in the annual estimates was modeled with linear regression, weighting survival estimates by the inverse of the standard error. Data for yearlings were pooled across years due to the low numbers that were radio-collared each year.

A yearling female might remain with its mother for a second year, be permanently separated in spring (usually at the birth of a new calf), or be temporarily abandoned until her mother's new calf dies. The affect of maternal attendance on yearling survival was estimated by using staggered entry and exit in the Kaplan-Meier procedure (Pollock et al. 1989), conditionally on whether it was accompanied by its mother. During May and June, yearlings were considered independent if they were abandoned anytime during that month and remained independent through the end of the month. The effect of age at death of a new calf (in days) on the rate at which maternal attendance was restored to the yearling was tested by rank-sum test with exact probability (Statistix, NH Analytical Software, Roseville, Minnesota, USA).

Parturition rates (proportion of adult females that gave birth each year) were calculated only from adult radio-collared females ≥4 years old that were sighted on each flight from 15 May to 30 June. Twinning rate was the proportion of adult females with calves that also had twins when first sighted with a calf. Twinning rate samples were augmented with observations of uncollared moose with calves during the telemetry flights prior to 4 June and by surveying areas not normally traversed in telemetry surveys. Calf sightings made within 1 km of previous sightings that year were excluded from the sample to avoid double counting (Testa et al. 2000c). Confidence intervals for proportions were calculated by bootstrapping (Efron 1982). Parturition rates of 3-yr-old females and females ≥4 years old, and twinning rate were modeled as response variables against covariates with logistic regression (Agresti 1990).

Modeled population growth.—In order to evaluate biases in estimated population parameters, estimates of the female population size (≥1 yr old) from 1994 to 2000 were compared to a bootstrap population model (Eberhardt et al. 1994). The bootstrapped population was initialized with the 1994 population estimate and five age classes corresponding to the first four year classes and adults ≥4 years old. The initial age structure was derived from the relative strengths of the previous calf:adult ratios and mean annual survival rates. Observations of survival of radio-collared moose were applied on a monthly basis to the corresponding age classes, with yearling data pooled across years. Parturition and twinning rates were applied annually using all available data from each year, but the proportion bearing their first calf at age 3 was based on the mean of the known-aged sample. A bootstrap sample was drawn from the radio-tracking observations to simulate sampling error at each time step and the resulting sample was resampled to simulate the fate of each individual in the population at that time step. The distribution of modeled population estimates (10 000 iterations) was compared to the estimates of female population size in the NSA.

A simpler, general model was used to evaluate the potential importance of predation on population growth. The female segment of the moose population was simulated in spreadsheet software (Microsoft Excel) using a formulation of the Euler-Lotka equation (Eberhardt and Siniff 1977, Eberhardt 1985). The commonly measured parameters of survival, age of first reproduction, and adult fecundity are related to population growth rate (λ) by

$$1 = \lambda^{-a} \times P0 \times P1 \times P^{a-2} \times F \times (1 - P/\lambda)^{-1}$$

where $P0$ = survival from birth to age 1, $P1$ = survival from age 1 to age 2, P = annual survival (excluding hunting mortality) thereafter, F = mean birth rate in female calves/adult female/yr, and a = age at first parturition.

This assumes that, following two years of juvenile mortality, adult mortality was relatively constant across
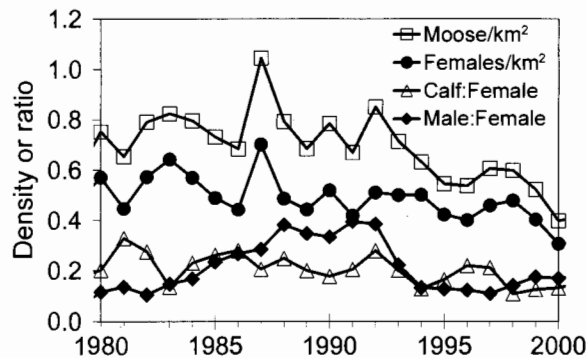
FIG. 2. Fall composition (calf:female and male:female ratios) and minimum densities of moose in Count Areas 13 and 14 in the Nelchina Study Area, south-central Alaska, from 1970 to 1999. The peak in 1987 is considered anomalous. It is nearly 50% higher than counts in the surrounding six years of data, and a very high concentration of moose in a small area of northern Count Area 14 in 1987 was probably due to temporary immigration (R. Tobey, *personal communication*).

age classes. Similarly, once maturity was reached, age-specific variation in fecundity was small and relatively unimportant. An even sex ratio at birth was assumed. These assumptions were considered conservative because the parameters were estimated from a sample representing a cross section of ages present in the population. The model also assumes a stable age distribution. A similar formulation to the above model, but incorporating a maximum age of 15 years (Eberhardt 1985), was also applied to confirm the assumption that growth rate is insensitive to maximum age with the parameter values estimated here. Sensitivities of λ to measurement uncertainty in each parameter were compared by holding the other parameters constant at their best estimate as the parameter of interest was varied across its 95% confidence interval. Expected growth from this model, using parameters estimated in the NSA, was compared to the potential rate of growth without predation and to potential growth with maximum fecundity. Growth rate without predation was estimated from the above model by treating predator-

caused mortality as censored data in survival estimates. This assumes that all predator-caused mortality was additive to other mortality causes and therefore represents an estimate only of the potential impact of predators on population growth.

RESULTS

Population ecology

Population trajectory of moose in the Nelchina Study Area.—The minimum density of adult female moose in the Count Areas (CAs) was generally stable (Fig. 2) from 1980 to 1993 (mean = $0.52/km^2$, $cv = 0.16$), but was lower during this study (mean = $0.42/km^2$, $cv = 0.15$, $t = 2.78$, df = 19, $P = 0.01$). The downward trend in total numbers beginning in the mid 1980s (Fig. 2) was mostly the result of declining proportions of males (due to increased harvest) and calves, but direct estimates of the density of females older than calves in the entire Nelchina Study Area (NSA) also have declined 50% since 1994 (Table 1). The change in density of moose in the CAs is less than that for the entire NSA, suggesting that the decline is greatest in the eastern part of the NSA, outside the CAs, where moose densities are lowest. The decline in numbers of female moose was preceded by a decline in calf:female ratios (Fig. 2). The ratio of calves to females from 1994 to 2000 was 33% below the average from 1980 to 1993 (0.23 vs. 0.16, $t = 3.33$, df = 19, $P = 0.002$).

Snow depths and browse.—Mean snow depths in late winter averaged 54 cm ($\pm$ 1 SE = 11, range 34–75 cm) and approached or exceeded the threshold for "severe" (74 cm; Coady 1974, Ballard et al. 1991) only in 1995 and 2000. There was a substantial amount of unutilized *S. alexensis* in the NSA. Most side stems were small, wilted, and rarely browsed (4–11%); terminal twigs were therefore the most important stems for moose in riparian areas. The winter utilization of terminal twigs of *S. alexensis* along the Oshetna River and Tyone Creek from 1995 to 2000 varied from 12% to 82% (Fig. 3). Utilization of terminal twigs was positively correlated with winter snow depth ($r^2 = 0.74$, $P = 0.0003$),

TABLE 1. Results of population estimates of the Nelchina Study Area and surveys in Count Areas 13 and 14 (2000 km²) within the Nelchina Study Area (4200 km²; see Fig. 1) from 1994 to 2000.

	Population estimates		Count Area surveys				
Year	Moose/km²	Females /km²	Moose/km²	Females/ km²	P(sighting)	Moose/km²	Females/km²
1994	0.81 (0.67–0.94)	0.60 (0.50–0.70)	0.63	0.50	0.69 (26)	0.91 (0.74–1.26)	0.72 (0.59–1.00)
1995	⋯	⋯	0.55	0.42	0.71 (38)	0.77 (0.65–0.95)	0.59 (0.50–0.73)
1996	⋯	⋯	0.53	0.40	0.76 (42)	0.70 (0.60–0.86)	0.53 (0.45–0.65)
1997	⋯	⋯	0.61	0.46	0.83 (29)	0.73 (0.88–0.63)	0.55 (0.48–0.67)
1998	0.57 (0.48–0.66)	0.44 (0.37–0.51)	0.60	0.48	⋯	⋯	⋯
1999	0.55 (0.46–0.64)	0.43 (0.36–0.50)	0.52	0.40	0.72 (39)	0.72 (0.61–0.92)	0.56 (0.47–0.71)
2000	0.39 (0.34–0.44)	0.30 (0.26–0.34)	0.40	0.31	0.71 (38)	0.56 (0.48–0.72)	0.44 (0.37–0.56)

Notes: The 95% confidence intervals are given within parentheses in columns 2, 3, 7, and 8. Apparent densities in the Count Areas (columns 4–5) are minimum estimates based on total counts at low search intensity. Columns 7 and 8 are densities adjusted for probability of sighting. Probabilities of sighting in Count Areas (column 6) are shown for years in which the number of radio-collared moose seen and those present in the Count Area (in parentheses) were determined.
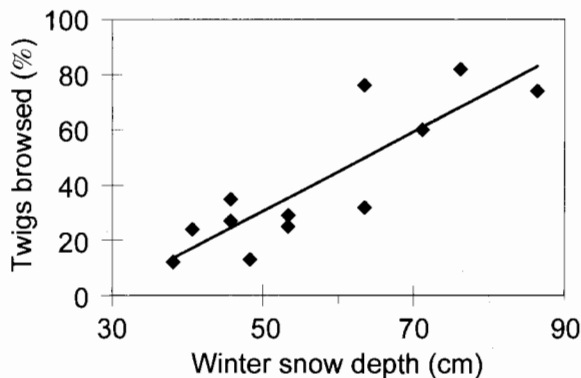
FIG. 3. Percentage utilization of terminal twigs of *Salix alexensis* by moose in the Oshetna River and Tyone Creek drainages in relation to mean snow depth in late winter in the Nelchina Study Area, Alaska, from 1995 to 2000. A depth of 74 cm is considered a severe winter (Coady 1974, Ballard et al. 1991).

suggesting that browse might become limiting in winters of deep snow.

Predator populations.—The density of independent brown bears (older than dependent cubs) in a 2150-km² portion of the NSA in 1998 was 21.3/1000 km² (95% CI 18.4–25.9; Testa et al. 2000c). This is in the higher range of brown bear densities for interior Alaska, where salmon are less available for consumption by bears than they are in coastal areas (Miller et al. 1997). Although hunting of brown bears in the study area accounts for most of their mortality, rates of harvest were near sustainable levels (~5%, Miller 1997; Testa, *unpublished data*), and therefore not likely to cause substantial changes in bear numbers in the relatively short period of this study.

TABLE 2. Estimated density of wolves (per 1000 km²) and harvest density (wolves harvested per 1000 km²) in the Nelchina Study Area. In 1994–1995 and 1996–1997, essentially all harvest took place before the population estimate in March.

Winter	Spring estimate	Winter harvest	Fall density†
1994–1995	4.5 (3.2–6.9)	4.2	8.7
1995–1996	9.9 (9.7–11.3)	0.0‡	9.9
1996–1997	5.9 (5.2–8.9)	6.4	12.3
1998–1999	···§	4.5	≥13.1
1999–2000	···§	7.2	≥14.5

Note: The 90% confidence intervals are given in parentheses.

† Fall density of wolves was calculated as the sum of the spring estimate and winter harvest, ignoring natural mortality, and is therefore conservative.

‡ In 1995–1996, due to unusually late snowfall, a harvest of 1.2 wolves per 1000 km² took place after the population estimate in February.

§ During 1998–1999 and 1999–2000, a minimum density was estimated from packs identified in moose composition and telemetry flights from October to February, with total harvest per 1000 km² shown.

TABLE 3. Rates of parturition and twinning of adult moose (≥4 years old) in the Nelchina Study Area, south-central Alaska (with sample sizes in parentheses), 1994–2000.

Year	Parturition rate (n)	Twinning rate (n)	Fecundity
1994	0.63 (40)	0.091 (77)	0.68
1995	0.86 (58)	0.126 (119)	0.97
1996	0.86 (68)	0.144 (139)	0.98
1997	0.87 (59)	0.212 (113)	1.06
1998	0.78 (52)	0.244 (82)	0.97
1999	0.90 (48)	0.180 (133)	1.07
2000	0.76 (54)	0.169 (130)	0.89
Total	0.82 (379)	0.166 (793)	0.97

Fall densities of wolves gradually increased from 1994 to 1999, but the magnitude of that change may be underestimated due to the uncertainty of counts since 1997 (Table 2). Due to the low, late harvest of wolves in the winter of 1995–1996, the effects of wolves on moose should have been greater in that winter and possibly the winter of 1996–1997 than in the winter of 1994–1995 when snowfall and harvest started earlier. No formal estimates of wolf density were made in late winters of 1998–1999 or 1999–2000 due to the absence of suitable snow conditions for tracking (Becker et al. 1998). However, minimum fall densities were consistent with an increasing trend (Table 2). The trend in harvest of wolves, especially in the last two years of study, also mirrored this upward trend in numbers (R. W. Tobey, *personal communication*).

Life history elements

Reproduction.—No moose gave birth before the age of 3 years in this study (n = 31) and only 13 of 22 moose reaching 3 years of age gave birth. All 11 moose reaching 4 years of age had borne calves by that age. Mass at 11 months of age did not affect the probability of giving birth at age 3 ($t = 0.521$, df = 18, $P = 0.30$, one-tailed).

Annual parturition rates averaged 0.82 ($\pm$ 1 SE = 0.037) among radio-collared females ≥4 years old from 1994 to 2000 (Table 3), but parturition rates varied significantly among years ($G^2 = 10.11$, df = 1, $P = 0.015$). The best fitting logistic regression model included the years 1994 and 2000, which were lower than average, as well as the number of calves accompanying the female the previous fall (Table 4). Twinning rates

TABLE 4. Logistic regression model predicting parturition rate among radio-collared moose in the Nelchina Study Area, south-central Alaska, in the years 1994 and 2000.

Variable	Coefficient	1 SE	G^2	P
Intercept	2.879	0.289	···	···
Fall calf	−1.660	0.296	30.890	0.000
Year 1994	−1.645	0.420	10.697	0.001
Year 2000	−1.292	0.411	9.212	0.002

Note: G^2 and P values are presented for sequential addition of listed variables (1 df) to the model.

TABLE 5. Logistic regression model predicting twinning rate among radio-collared moose in the Nelchina Study Area, south-central Alaska, from 1994 to 2000.

Variable	Coefficient	1 SE	G^2	P
Intercept	−3.183	0.589	...	...
Fall calf	−2.130	0.644	13.704	0.0002
Previous twins	1.771	0.461	14.875	0.0001

Notes: G^2 and P values are presented for sequential addition of listed variables (1 df) to the model. The analysis was limited to only those moose that were parturient in consecutive years.

of all moose seen with calves (Table 3) varied from 0.09 to 0.24 and were best modeled as an increasing trend in the seven years studied ($G^2 = 4.03$, df = 1, $P = 0.045$), a period of declining population density. Winter snow depths in either of the preceding two winters did not explain the variation in parturition rate or twinning ($P > 0.75$). When only radio-collared females were analyzed, the annual trend toward increased twinning was undetectable with the smaller sample, but the number of calves accompanying a female in fall significantly reduced twinning rates among parturient females the next spring ($G^2 = 9.30$, df = 1, $P = 0.002$). When the analysis was limited to females that were parturient in successive years, the number of calves born the previous year was positively related and the number of calves accompanying the female in fall was negatively related to rate of twinning in the second year (Table 5). In other words, propensity to have twins was an individual trait, but rearing either calf to fall was detrimental to fecundity the following year.

Survival.—Females ≥2 years old had a mean annual survival (May–April) of 0.92 (± 1 SE = 0.014) from April 1994 to July 2000 with heaviest mortality in calving season and late winter. Survival was very high in 1994 and 1995 (0.98 and 0.96) but declined to ~0.91 in the remaining years. Both linear and quadratic terms entered a stepwise ($P < 0.05$) linear regression model ($y = 1.025 - 0.046x + 0.0045x^2$).

Of 35 deaths occurring from March 1994 to July 2000, 21 were clearly attributable to predators (10 to wolves, 6 to brown bears, and 9 to unknown predators). Four deaths were from unknown causes, but predation could not be excluded in three of those. Other known causes of death included dystocia (one pair of twin calves stuck in birth canal), accidental injury (1), and winter starvation (2). Adults with a calf showed a trend toward higher mortality than those without a calf (Table 6; $Z = 1.492$, $P = 0.136$). After censoring nonpredation deaths, mortality attributable to predation or suspected predation was significantly greater among females tending a calf (10% vs. 4%, $Z = 2.058$, $P = 0.040$).

Annual survival of yearlings independent of maternal attendance (Table 7) was 0.80 (± 1 SE = 0.06). All nine yearling deaths occurred in spring to midsummer (early May to early August). Three were attributed to wolves and two to brown bears. Cause was uncertain in the other four, but predation was considered the most probable cause because of the apparent health of the moose when previously observed and proximity of a predator to the freshly dead carcass. Female yearlings abandoned by their mothers suffered higher mortality than yearlings that were able to maintain that association (0.33 vs. 0.09, Table 7, $Z = 2.054$, $P = 0.040$). Survival and abandonment of yearlings were unrelated to yearling's body mass as a calf in April (t tests, $P > 0.47$). Nine of 12 (75%) nonparturient females with yearlings kept their yearling to at least August. Those disappearing in August were males that may have been legally harvested at that time.

Age of the new calf at death may influence rate of reassociation between yearlings and mothers ($P = 0.058$). All reassociations took place when calves died in <10 days (2, 7, and 10 d), while two opportunities

TABLE 6. Comparison of survival rates of female moose in the Nelchina Study Area, south-central Alaska, from March 1994 through July 2000, conditional on the presence of a calf.

Month (days)	Females alone			Females with calf		
	At risk	Died	Survival (1 SE)	At risk	Died	Survival (1 SE)
5 (12–21)	391	0	1.00 (0.00)	46	0	1.00 (0.00)
5 (22–31)	220	0	1.00 (0.00)	220	0	1.00 (0.00)
6 (1–10)	187	0	1.00 (0.00)	253	5	0.98 (0.01)
6 (11–20)	214	1	1.00 (0.01)	220	1	0.98 (0.01)
6 (21–30)	284	0	1.00 (0.01)	163	1	0.97 (0.01)
7	269	2	0.99 (0.01)	122	3	0.95 (0.02)
8	291	1	0.98 (0.01)	87	0	0.95 (0.02)
9	292	1	0.98 (0.01)	86	0	0.95 (0.02)
10	284	2	0.97 (0.01)	82	0	0.95 (0.02)
11	222	3	0.96 (0.01)	88	0	0.95 (0.02)
1	319	2	0.96 (0.01)	92	1	0.94 (0.02)
2	323	1	0.95 (0.01)	85	0	0.95 (0.02)
3	322	3	0.94 (0.01)	100	2	0.92 (0.02)
4	340	3	0.93 (0.01)	92	3	0.89 (0.03)

Note: Data are pooled across years, with staggered entry and exit due to new captures and temporary emigration.

TABLE 7. Survival of yearling female moose in the Nelchina Study Area, south-central Alaska, in the years 1995–2000.

Month	At risk	Died	Survival (1 SE)
All yearlings			
5	47	1	0.98 (0.02)
6	45	4	0.89 (0.05)
7	39	3	0.82 (0.06)
8	35	1	0.80 (0.06)
9–12	34–36	0	0.80 (0.06)
1–4	36–37	0	0.80 (0.06)
Yearlings with mother			
5	33	0	1.00 (0.00)
6	21	1	0.95 (0.05)
7	21	1	0.91 (0.06)
8	18	0	0.91 (0.06)
9–12	18	0	0.91 (0.06)
1–4	19–20	0	0.91 (0.06)
Independent yearlings			
5	13	1	0.92 (0.07)
6	22	3	0.80 (0.09)
7	18	2	0.71 (0.10)
8	17	1	0.67 (0.10)
9–12	15	0	0.67 (0.10)
1–4	15–16	0	0.67 (0.10)

TABLE 8. Survival of calves born to radio-collared moose in the Nelchina Study Area, south-central Alaska, in the years 1994–1999. Survival in months 5–6 is an estimate from parturition to the end of June.

Month	At risk	Deaths	Survival (1 SE)
5–6	347	229	0.34 (0.03)
7	114	24	0.27 (0.02)
8	91	3	0.26 (0.02)
9	87	0	0.26 (0.02)
10	92	1	0.26 (0.02)
11	92	6	0.24 (0.02)
1	96	4	0.23 (0.02)
2	92	2	0.23 (0.02)
3	90	3	0.22 (0.02)
4	82	6	0.20 (0.02)

for reassociation were missed in that period (8 and 10 d) and no reassociations occurred when calves died after 10 days of age ($n = 5$). In the three cases where yearlings rejoined their mother, reassociation took place within 1–3 days of the calf's death.

The average rate of calf survival from May to October in this study (0.26; Table 8) was lower than that observed by Ballard et al. (1991) in 1977–1978 and 1984 (0.39, $P = 0.004$). Interannual variation in calf mortality to August was not significant from 1994 to 1998 (Testa et al. 2000a). Ballard et al. (1991) reported that most moose calves were killed in the first 60 days of life and over 70% of mortality from May to October was caused by brown bears. Age-specific mortality of calves from 1994 to 1998 was essentially a linear, declining function of calf age from a rate of 4% per day at birth to nearly zero at 64 days (Testa et al. 2000a). Sequential comparisons of annual estimates of calf survival to the pooled survival of remaining years (1994–2000) failed to identify any year as an outlier ($P \geq 0.067$). Calves were not radio collared, so cause of death usually was unknown. However, occasionally the dead calf was observed or the fate of the mother led to presumptive causation. Brown bears (6), wolverine (1), and eagles (1) were implicated as predators on known individuals, though wolves also were observed pursuing unmarked female–calf pairs in spring. Mortality of calves for the remainder of the year was low, with a small surge in late winter (Table 8).

Modeled population growth

The median annual population growth rate (λ) in the NSA, as modeled by bootstrapping data from the radio-collared sample of female moose was 0.96 (95% CI =

0.93–0.99), consistent with the occurrence of a decline in numbers that was observed in surveys, but smaller than actually occurred ($\lambda = 0.89$). The bootstrap probability of overlap with the 95% confidence interval of the 2000 estimate of adult females was only 0.0004. Growth rate of a population with a stable age structure using estimated mean rates of annual survival and fecundity (Eberhardt and Siniff 1977) was 0.99 and was most sensitive to measurement uncertainty in adult survival (Fig. 4). The difference between modeled and observed population growth could result from bias in the estimation of parameters, especially adult survival, from radio-collared moose, or a difference in the spatial distribution of the source data being compared. There was a preponderance of radio-collared moose in areas of high moose density, particularly in the traditional Count Areas (Table 1) where the decline was inter-
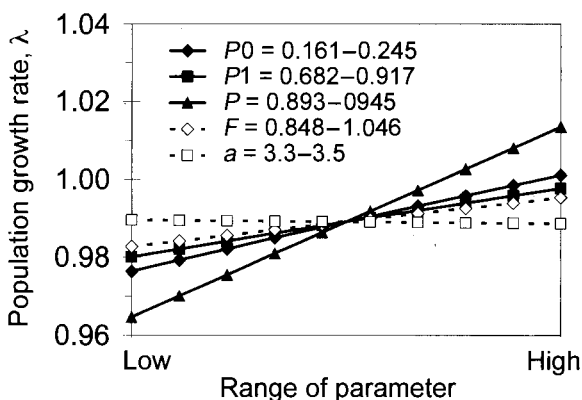

FIG. 4. Sensitivity of population growth rate (λ) to uncertainty in model parameters (Eberhardt 1977, Eberhardt and Siniff 1977) estimated from female moose in south-central Alaska. Parameters are annual survival rates of calf ($P0$), yearling ($P1$), and "adult" moose (>1 yr old, P), age of first calving (a), and adult fecundity (F). Sensitivities of λ to measurement uncertainty in each parameter were compared by holding the other parameters constant at their best estimate as the parameter of interest was varied across its 95% confidence interval, except for fecundity, which was varied across the range of annual estimates. "Low" to "High" on the abscissa corresponds to the values in the key.

mediate in magnitude ($\lambda = 0.923$). The NSA estimates included large areas of low density to the east that were poorly represented in the radio-collared sample. The discrepancy between modeled and estimated population size, coupled with the smaller decline in the Count Areas (Table 1) suggest that a greater population decline has occurred in areas of lower moose density.

If the proportion of calf mortality from nonpredation causes (Ballard et al. 1991) is used to adjust calf survival estimates observed in this study, expected annual calf survival would be ~0.81. Adjustments to yearling and adult survival were made to the data in this study by censoring all predation-caused mortality, yielding estimates of 1.00 and 0.98. Assuming that yearling survival was no greater than that of adults, the modeled stable rate of growth of a population with these parameters (Eberhardt and Siniff 1977) was $\lambda = 1.21$. While the assumption that mortality due to predation is additive to that from other sources may not be wholly true, the degree of compensatory mortality that would be required to prevent strong population growth in the absence of predation is extreme. In contrast, increasing fecundity to near a theoretical maximum for moose (0.9 female calves/female) only increased the expected growth rate of this model from $\lambda = 0.99$ to $\lambda = 1.04$ when mortality was maintained at observed rates, or $\lambda = 1.06$ if age of first reproduction also was reduced to two years.

DISCUSSION

Population dynamics

Ultimately, the same ecological pressures that drive population dynamics of moose should be reflected in the life history attributes of individuals, including the trade-offs in reproductive effort and survival. At the population level, the picture that emerges in the Nelchina Study Area (NSA) is of a moose population moderately affected by nutritional limits on its reproductive potential, but primarily limited in its capacity for growth by mortality from predation. Pregnancy rate was typical for the species (Heard et al. 1997, Berger 1999), while twinning was low and age of first reproduction was high (Boer 1992, Gasaway et al. 1992). At least one preferred forage species, *S. alexensis*, was underutilized in most winters (Fig. 3), and though it was more heavily browsed when snow was deeper, there was no discernable effect of snow depth on parturition or twinning rates of moose. Underutilized winter browse, unrealized potential rates of conception (Testa and Adams 1998), and the importance to ovulation rates of both body condition and forage in fall (Gunn and Doney 1975, Testa and Adams 1998) suggest that forage from spring to fall may constrain productivity of moose in the NSA more than winter forage in most years.

Ballard et al. (1991) concluded that predation on moose, particularly on calves, was the most important factor limiting moose population growth in the Nelchina Basin. From 1977 to 1984, predation was particularly heavy on young calves and attributed primarily (73%) to brown bears (Ballard et al. 1981, 1991). Starvation was the primary cause of winter mortality of calves and yearlings, but it was concentrated in a single particularly harsh winter and nearly absent in others. Experimental removal of brown bears in one year significantly improved fall calf recruitment (Ballard and Miller 1990). Predation was the cause of 8 of 11 adult female fatalities where cause could be determined, but 10 others died from unknown causes (Ballard et al. 1991). Both yearling and adult female mortality from 1976 to 1986 were substantially lower (5%) than observed in this study (Ballard et al. 1991). Without changes in seasonal timing of calf mortality, density of brown bears, or improvement in moose mortality rates in comparison to those results, there is little reason to revise Ballard et al.'s (1991) conclusion that predation by brown bears is important in limiting growth of the moose population.

While preying primarily on moose, wolves at spring densities of 3–8 wolves/1000 km^2 and moose:wolf ratios >164 did not prevent slow growth of the moose population in earlier work (Ballard et al. 1987). Wolf densities increased in the period of this study to levels higher than reported from 1975 to 1982, when moose were declining (Ballard et al. 1987), but were still in the "moderate" range in comparison to other North American studies (Ballard and Van Ballenberghe 1998). Caribou, which overwintered in the Nelchina Basin during previous studies, were virtually absent during winter in this study, which is likely to have increased the reliance of resident wolves on moose over that observed by Ballard et al. (1987, 1991).

Estimates of moose consumption by bears in GMU 13 (Ballard and Miller 1990, Ballard et al. 1990) were made during the seasonal influx of caribou, yet still indicated consumption >5 moose calves/bear and 1.4 adult moose/bear in June and July alone. Boertje et al. (1988) found continued predation on adult moose, primarily by male brown bears, into the fall in a population of moose at very low density (<0.1 moose/km^2), also with caribou present. The presence of caribou as alternative prey does not appear to prevent brown bears from consuming moose at per capita rates that rival those of wolves, though that consumption is skewed heavily toward calf moose in summer.

Reported annual kill rates for bears and wolves are similar when age and sex classes are combined (Boertje et al. 1988, Fuller 1989, Ballard et al. 1990, Hayes et al. 2000, Hayes and Harestad 2000), so that a single prey:predator ratio, as suggested by Gasaway et al. (1992), can give a rough idea of predation pressure. The ratio of moose to large predators in the NSA declined from ~27 in 1994 to ~15 in 1999. Applying Keith's (1983) model, an optimistic rate of moose population growth ($\lambda = 1.21$) in the absence of predation

in the NSA, and a conservative predation rate (7 moose/predator/yr), yields an estimate of the sustainable ratio of moose to predators (7/0.21 = 33.3) that is well above the ratios occurring during the period of this study. Prey:predator ratios as a measure of predation impact offer only a rough idea of population processes (Theberghe 1990). However, common estimates of threshold ratios below which prey populations should decline (Keith 1983, Fuller 1989, Gasaway et al. 1992, Eberhardt and Peterson 1999) substantially exceed those observed here and are consistent with the high rates of mortality, particularly in summer calves, and the decline of moose numbers observed in the NSA.

While nutritional constraints on the moose population in the NSA were important, the potential for population growth with the observed parturition and twinning rates was still high. That predation mortality is primarily additive has been supported in GMU 13 at similar population density and predation intensity (Ballard et al. 1991), and in other parts of Alaska and Yukon (Gasaway et al. 1992, Hayes et al. 2000). Models incorporating the observed life history trade-offs (Testa 2004) also suggested that improved calf production could accentuate mortality of adults and yearlings from predation, reducing expected gains in population growth rate. From a management perspective, therefore, methods that improve range conditions and, by extension, moose productivity in the NSA have limited potential to reverse the decline of moose numbers when compared to measures that reduce predation. From the perspective of a female moose, predation risk should be an important factor affecting life history strategies in the NSA.

Life history trade-offs

Among radio-collared moose in the NSA, the phenotypic trade-off between successful rearing of a calf to fall and subsequent calving and twinning suggests that nutritional constraints affect life history trade-offs in the NSA. The positive correlation observed between twinning in successive years (Table 5) could reflect either genetic predisposition to twinning in some individuals, or age-specific effects (Sæther and Haagenrud 1983; Testa, *unpublished data*). That increasing density and winter severity can increase the phenotypic cost of reproduction was demonstrated in red deer (*Cervus elaphus* L.; Clutton-Brock et al. 1987b). Where moose in Scandinavia were kept well below K (carrying capacity) by human hunting, the negative effects on pregnancy and ovulation rates were undetectable (Sæther and Haagenrud 1983, Sand 1998). In poorer habitats both body fat and subsequent fecundity of moose were significantly less following lactation (Testa and Adams 1998, Keech et al. 2000).

A correlation between predation and reproductive condition has not previously been demonstrated in an ungulate species. That reproductive effort might increase rates of adult mortality to predation is implied by antipredator behaviors shown by female moose with calves (Edwards 1983, Stephens and Peterson 1984, Molvar and Bowyer 1994, White and Berger 2001), and an effect on adult survival has been suggested in moose (Boertje et al. 1988, Larsen et al. 1989), as well as other ungulates (Estes 1966, Berger 1991, Bleich et al. 1997, Bowyer et al. 1998, Kie 1999, Whittaker and Lindzey 1999). The correlations between adult reproductive effort and predator-caused mortality among adult moose and their previous calves in this study are therefore significant. While poor adult body condition might contribute to adult vulnerability to predators, poorly conditioned adult moose in this study were least likely to have calves (Testa and Adams 1998), so risk of predation in early summer would appear to relate directly to the presence of the calf rather than to the condition of the female. By autumn, body condition and presence of a calf are confounded, so that indirect effects of nutrition on predation in winter cannot be excluded. However, the greatest difference in mortality rates occurred in summer.

The absence of even a weak correlation between yearling mass and subsequent mortality of yearlings suggests that nutritional effects on vulnerability play little role in the phenotypic trade-off between present and previous reproductive effort. White et al. (2001) found little difference in vigilance behavior or distance from cover between independent yearlings and those accompanied by their mother in the summer, suggesting that newly independent yearlings are slow to make the adjustments necessary to avoid predators on their own. Ballard et al. (1991) found higher yearling mortality during winter than was evident in our study, most of it from starvation during a single winter of deep snowfall. Under those conditions, nutritional constraints stemming from maternal investment in calf growth might play a larger role in yearling vulnerability to predation.

That extending maternal care increases the survival of yearling moose supports the contention that predation is an important selective force in the evolution of matrilineal groups in ungulates (Clutton-Brock et al. 1982:194). The Alaskan subspecies of moose, *A. alces gigas*, occupying the most northern and open habitats in the range, is the most social of the species, often forming small groups in winter and summer, and large harems during fall breeding (Miquelle et al. 1992, Van Ballenberghe 1992, Molvar and Bowyer 1994). Little evidence has been offered that sociality in moose includes kinship or matrilineal groups, but home range studies suggest that, upon independence, female offspring tend to occupy home ranges overlapping that of their mother (Ballard et al. 1991, Hundertmark 1998). In one instance during this study, a female moose was observed to maintain a close association with her yearling even in the presence of her new calf, forming a matrilineal group of three that successfully avoided predation for the next year. If maternal relations and

age of successive offspring provide a social hierarchy (Clutton-Brock et al. 1982) that alleviates the agonistic costs of group foraging (Molvar and Bowyer 1994), the advantages to group foraging may be enhanced among related individuals.

The similarity in expression of top-down and bottom-up factors in both population-level vital rates and their life history counterparts in moose leads to the question of whether phenotypic life history trade-offs contribute significantly to population dynamics. One prediction following from these results is that negative covariance of fecundity between years would increase at high densities and contribute to higher interannual variability in fecundity. Another is that without bottom-up costs of reproduction (i.e., at low density), the observed top-down trade-offs are equivalent to lowering average survival of all classes, but when both trade-offs occur it can alter the expected population growth rate (Testa 2004). Using the bottom-up trade-offs observed in moose, Testa (1998) found that part of the increase in population growth obtained by reducing predation on calves might be offset by the interaction with bottom-up trade-offs in fecundity. Testa (2004) simulated a similar, but more general, set of ungulate life history trade-offs under a variety of predation scenarios and found their interaction to be mildly anti-regulatory. A few studies hint at more complex dynamics that might result from density dependence and optimum life history strategies involving predation (Dehn 1994, Ruxton and Lima 1997, Kokko and Ruxton 2000). The lesson and challenge of these studies is that population-level ecology and longitudinal studies of individuals are complementary, and their interplay can provide greater insight both to the mechanisms of population change and to the selective forces affecting life histories.

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