Ecology, 85(5), 2004, pp. 1453–1459

INTERACTION OF TOP-DOWN AND BOTTOM-UP LIFE HISTORY TRADE-OFFS IN MOOSE (*ALCES ALCES*)

J. WARD TESTA[1]

Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska 99518 USA

Abstract. Moose (*Alces alces*) in south-central Alaska have been found to have phenotypic life history trade-offs that can be partitioned into the same "bottom-up" and "top-down" trophic framework often applied at the population level. The potential interaction of these life history trade-offs was studied under varying degrees of predation and nutritional limitation using models based on data from radio-collared moose in south-central Alaska. The interaction was mildly antiregulatory, assuming that bottom-up trade-offs are density dependent. That is, as nutritional constraints increased, a female that skipped reproduction after successfully rearing a calf enhanced the survival of herself and her yearling enough in the second year to overcompensate for the loss of productivity. In a declining population, the reverse could occur, accentuating the decline. A more general, stage projection matrix was used to model a broader range of predation rates in summer and winter, in order to contrast the potential importance of bears (*Ursus arctos* and *U. americanus*) and wolves (*Canis lupus*) in such an interaction. The greatest effect of life history interactions on population growth occurred with moderate predation in summer and heavy predation in winter. Relative to direct ecological effects on survival and reproduction, the influence of such an interaction was relatively weak. However, subtle effects on the stability of predator–prey interactions, particularly those involving bear predation, cannot be excluded because of the antiregulatory nature of the interaction and uncertainties about class-specific vulnerability to predation in other settings. These findings underscore the relevance of understanding the alternative life history choices that arise from interactions in both directions on the food chain, particularly given that the top-down trade-offs are usually poorly known.

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

INTRODUCTION

The study of life history trade-offs is usually the purview of evolutionary biologists seeking to understand life history evolution. The interaction of phenotypic life history trade-offs and population dynamics is often neglected, either because population studies do not resolve longitudinal variation in individuals, or population dynamics are not directly examined in evolutionary studies at the individual level. Nevertheless, the phenotypic expression of life history strategies may help to explain variation in population dynamics of mammals and other taxa. For example, density-dependent regulation of a population might be attributed to declining fecundity in response to resource shortage (e.g., Messier et al. 1988), but fecundity might be reduced uniformly among all reproductive classes or by increased interbirth intervals of individuals that successfully rear offspring to independence (Testa 1987, 2004, Clutton-Brock et al. 1989). The latter can cause greater interannual variability and time lags in fecundity (Testa 1996) that would be unpredictable without longitudinal data from individuals.

Determining the relative importance and interaction of nutritional, or "bottom-up" limits vs. predator-determined, or "top-down" limits on populations has been a central theme in many ecological studies (Hairston et al. 1960, Gutierrez et al. 1994, Berryman et al. 1995, Sinclair et al. 2000), but has not usually been applied in studies of life history trade-offs. This is especially true for empirical studies of top-down life history trade-offs: those involving explicit risks of predation resulting from reproductive effort. In a population of moose (*Alces alces* L.) in south-central Alaska, bottom-up and top-down life history trade-offs for individuals mirrored the effect of these factors at the population level (Testa 2004). In a population with moderate nutritional constraints and heavy predation, the cost of rearing a calf to the fall (a period of five months) was a 20–60% reduction in subsequent fecundity (Testa 1998, Testa and Adams 1998). In the same population, females with a calf experienced greater rates of predation, while newly independent yearlings suffered nearly four times the mortality of yearlings that received an additional year of maternal protection (Testa 2004). The effect of predation at the population level may therefore be complicated by its effect

Manuscript received 25 October 2002; revised 24 September 2003; accepted 24 September 2003. Corresponding Editor: G. M. Henebry.

[1] Present address: National Marine Fisheries Service, c/o Marine Mammals Management—USFWS, 1011 E. Tudor Road, Anchorage, Alaska 99503-6199 USA.
E-mail: Ward.Testa@noaa.gov

on phenotypic life history trade-offs. Predation on neonatal calves affects lactation burden and the magnitude of bottom-up constraints on fecundity on the one hand, but the resulting reproductive rates influence vulnerability of yearling and adult classes to predation (Testa 2004). The differing seasonality of predation by bears (*Ursus arctos* L. and *U. americanus* Pallas), which den in winter, and wolves (*Canus lupus* L.) also suggest that their respective impacts in such an interaction with bottom-up life history trade-offs may be different.

The life history trade-offs that I observed in moose (Testa 2004) lead me to question the effects of life history trade-offs on population dynamics of moose under varied scenarios of top-down and bottom-up pressures. I hypothesize that the interaction of realistic life history trade-offs has the potential to alter the expected dynamics of moose, and possibly other ungulates subject to both bottom-up and top-down ecological constraints. To test this, I focus on the interaction of top-down and bottom-up forces by modeling population growth rates under various combinations of nutritional and predator effects on individual life history trade-offs. The strength of such interactions is most likely to vary as the population approaches or retreats from carrying capacity (K; McCullough 1979), and as predator impact increases with decreasing ratios of prey to predator (Arditi and Ginzburg 1989, Gasaway et al. 1992), circumstances relevant to the dynamics of moose in North America (Gasaway et al. 1992, Hayes and Harestad 2000, Hayes et al. 2003) and possibly other ungulates.

Methods

The basis of the models used here is a stage-structured approach that partitions adult females into those having offspring and those that do not. The life history trade-offs produce differing reproductive and survival rates in these two classes and their offspring, and model iteration produces changes in the composition and growth of the population that can differ from models without this structure (Testa 1998). Without explicitly incorporating predator–prey interactions, I examined how the expected changes in composition resulting from top-down and bottom-up life history trade-offs could produce an interaction that affects population growth rate. This was done using life history traits very close to those observed in a population of moose in south-central Alaska (Testa 2004), then for more generalized parameters under varying nutritional constraints and intensities of predation in summer and winter. The seasonal partitioning of mortality was a means of separating the likely predatory impact of bears, which preyed heavily on moose during the spring and summer, from that of wolves, which were most effective in winter.

Female moose were first modeled using differences in mortality among age and reproductive classes that were reported by Testa (2004) while varying the reproductive trade-offs affecting parturition and twinning rates, extending an earlier approach (Testa 1998). The model was implemented in spreadsheet form (Microsoft Excel) with four age classes: yearlings (12–24 mo), 2-yr-olds (25–36 mo), nulliparous 3-yr-olds (37–48 mo), and adults ($\geq$3 yr). Yearlings were classified as independent or accompanied by their mother. Adults were classified as having zero, one, or two calves. Those having no calves were further divided into those that had borne the cost of lactation (i.e., a calf surviving to the end of September or later) and those that had lost calves earlier or not given birth that year. Calves were accounted for through the reproductive status of adult females and recruited into the female yearling population, assuming an even sex ratio.

Baseline rates of survival and reproduction in all categories were based on radio-collared moose in south-central Alaska (Testa 2004). To account for the rapid changes in population composition that occur after calving, the models were iterated in 5-d increments from 25 May, the median birthdate, until the end of July, then monthly except for December. At the start of an annual cycle, the two yearling classes were incremented by the number of surviving calves from the previous year, depending on the parturition rates expected of their mothers. Most abandoned yearlings became independent, but half of adult females that lost their new calf within 10 days after birth reacquired their yearling (Testa 2004). Maximum rates of adult parturition and twinning in the model were 0.9 and 0.2, respectively. Sixty percent of females reaching three years of age were assumed to have their first calves at that age and all first-time breeders (aged 3 and 4 yr) gave birth to single calves. At each time step, every age/reproductive class was subjected to the mortality rate for that class and period based on radio-tracking data (Testa 2004). Following this mortality, adult classes were adjusted to reflect the mortality of calves. Estimates of calf survival from 1994 to 1997 (Testa et al. 2000) were used in the model because of the greater temporal resolution in those years, and produced slightly higher annual survival (0.23) than that given by Testa (2004). Half of twin calves that died in the first 15 days were assumed to die together up to that age, but independently thereafter (Testa et al. 2000).

The models were iterated for 20 annual cycles based on trials to determine that the stage structure of the simulated population was stable by that point. The finite rate of population growth (λ) was determined from growth in the final year, while the ratio of calf to noncalf females in fall and reproductive parameters in spring were monitored to confirm the consistency of the models with survey data (Testa 2004). The bottom-up costs of reproduction were modeled by varying diminished rates of parturition and twinning in steps from 100% to 0% of their maximum rates in females that successfully reared a calf to the fall. Maximum rates were assigned to all other adult females. For a con-

TABLE 1. Elements of a stage projection matrix describing a generalized moose life history of three age classes and two yearling and adult states.

$$\begin{bmatrix} 0 & 0 & 0 & 0.5 \times S_{A1}S_C W_{A1} W_C (1-d) \\ 0 & 0 & 0 & 0.5 \times S_{A1}S_C W_{A1} W_C d \\ 0 & 0 & 0 & S_{A1}S_C W_{A1} d \\ S_{YA}W_{YA} & S_{YM}W_{YM} & S_{A0}W_{A0} & S_{A1} \times (S_C W_{A1}[1-d] + [1-S_C]W_{A0}) \end{bmatrix}$$

Notes: The population vector consisted of yearlings alone (YA) and with their mother (YM), and adults without (A0) and with a calf (A1). Calves (C) were tracked through the adult class A1. Survival (1 − mortality rate in Table 2) was separated into summer (S) and winter (W) components for each class. All yearlings reproduced in their second year. The maximum reproductive rate ($R = 1$) for adults was reduced by the proportion d (cost of reproduction) for adults with calves that survived the previous summer.

trasting null model, the same parameters without top-down mortality trade-offs were used, assuming a mortality schedule that minimized maternal risk (i.e., the higher survival of adults and lower survival of yearlings).

In order to investigate a broader range of predation pressures than observed in the Alaskan moose population, it was necessary to simplify the life history. A stage-projection matrix was devised to allow simple manipulations of predation pressure while encompassing bottom-up and top-down life history trade-offs similar to those observed in Alaskan moose (Table 1). The model population was composed of two classes each of yearlings and adult females (≥2 years old), with calves accounted for through the reproductive status of the adults. Yearlings either became independent after one year or remained with their mother if she failed to reproduce that year. An even sex ratio one year after birth was assumed. Top-down trade-offs were excluded in the null model by minimizing maternal risk, assigning a high baseline rate of survival to all adult females and a lower survival to all yearlings, as with the previous model. The alternative model included top-down trade-offs that enhanced yearling survival when yearlings remained with their mother, and decreased survival of adults when accompanied by a calf. I varied predation on all classes by increasing a scalar multiplier that was applied to baseline mortality rates (Table 2). In this way, the mortality rate of every class relative to the others remained constant while predation pressure on all moose was varied. Similarly, I simulated a range of bottom-up constraints on reproduction that prescribed the proportion (0–100%) of females that reared a calf to fall and subsequently skipped reproduction in the following year. Mortality was applied twice annually to simulate summer mortality (primarily bear predation) that occurred before the energetic burden of lactation, followed by winter mortality (primarily by wolves after bears retired to winter dens), which would not affect the energetic cost of lactation. I varied winter and summer predation levels separately and together to understand how wolves and bears might affect the population dynamics of moose differently. The stable population growth rate was used as the response variable, and the ratio of the growth rate of the model with top-down trade-offs to that of the null model (λ_T:λ_N) was graphed as a response surface relative to continuous scales of predation pressure and bottom-up costs of reproduction.

RESULTS

The initial model of life history interactions was intended to explore how the changing composition of the population caused by bottom-up costs of reproduction might interact with observed mortality rates that are driven by top-down reproductive costs as observed in

TABLE 2. Rates of mortality used in simulations to compare growth of moose populations with and without top-down life history trade-offs of varying severity.

	Summer (S) predation		Winter (W) predation	
Class	Light	Heavy	Light	Heavy
Calves (C)	0.10	0.90	0.10	0.90
Yearlings alone (YA)	0.04	0.36	0.04	0.36
Yearlings with mother (YM)	0.01	0.09	0.02	0.18
Adult alone (A0)	0.005	0.045	0.01	0.09
Adult with calf (A1)	0.010	0.10	0.02	0.18

Notes: The severity of predation was controlled by a scalar multiple (d) applied to the lowest rates of mortality to produce a range up to the highest rates shown. In this way, the relative rates of mortality, and therefore the state-dependent trade-offs in life history, were held constant while varying the level of predation across all classes. The null model employed only the lower of the two rates for adult females (S_{A0} and W_{A0}), and the higher of rates (S_{YA} and W_{YA}) for yearlings.

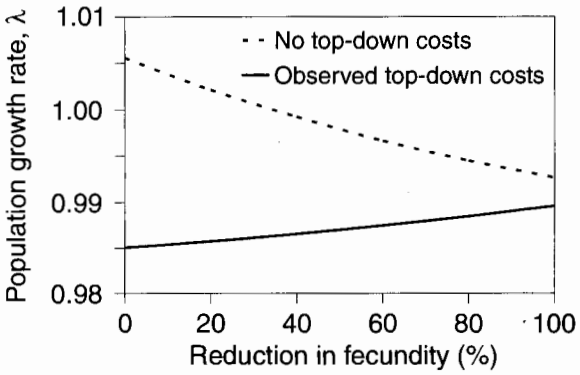


FIG. 1. Growth rate (λ) of model populations incorporating bottom-up and top-down life history trade-offs of moose. Fecundity was reduced by the amounts shown among females that had reared a calf to the previous fall and had therefore borne the energetic cost of lactation. Contrasting growth rates are shown for a null model of no top-down costs of reproduction based on mortality rates that minimized maternal risks (higher adult survival and lower yearling survival) and for a model including mortality trade-offs that enhanced yearling and adult survival when the mother skipped reproduction and tended her yearling an additional year.

Alaskan moose (Testa 2004). When the bottom-up cost of rearing a calf to fall was a 40% reduction in parturition and twinning rates, the modeled rates of parturition and twinning were close to the average rates observed (Testa 2004). With the starting parameters, fecundity varied from 1.08 to 0.85 as the bottom-up cost of reproduction was increased from 0% to 100%. The loss of reproductive output imposed in the null model by the life history trade-off in calving success was fairly small at the high rates of calf mortality and adult survival observed (Testa 2004), which is consistent with the relative insensitivity of λ to fecundity in that study. The inclusion of top-down life history trade-offs in the model dampened the effect of bottom-up trade-offs and caused the correlation between bottom-up reproductive costs and population growth rate to change sign (Fig. 1). That is, the model predicts that the effect of the interaction between top-down and bottom-up life history trade-offs observed in moose (Testa 2004) is mildly antiregulatory, with a maximum net effect on λ of ~0.02 (Fig. 1).

Baseline rates of survival in the generalized life history model were chosen so that the scalar term used to simulate heavy predation produced mortality rates similar to the highest reported in the literature for North American moose, while the magnitude of top-down trade-offs were similar to those observed among radio-collared moose in south-central Alaska (Testa 2004). Bottom-up costs of reproduction in the form of reproductive pauses following lactation reduced population growth substantially when predation was light, but had much less effect on population growth as predation increased (Fig. 2, left column). Growth rates of the null models (high adult and low yearling survival) were usually greater than the models that included top-down trade-offs in survival. However, the null models here do not represent an observed strategy so much as a standard of mortality that excludes top-down costs of reproduction by assuming minimal maternal risk. Using average rates of yearling and adult survival would shift the response surfaces up, but it is the slope of the ratio of growth rates (λ_T:λ_N, Fig. 2, right column) that is of interest. These response surfaces show positive slopes relative to increasing bottom-up costs of reproduction and negative slopes relative to increasing predation (Fig. 2, right column). That is, the interaction produced lower than expected growth when nutritional constraints on sequential reproduction were small, and higher growth as those constraints increased, relative to models that omitted trade-offs in predation risk. Winter predation tended to have the greatest effect on this interaction when predation was heavy (Fig. 2, top right). This occurred through the enhancement of both yearling and adult survival when reproductive pauses occurred, even though such pauses decreased calf production and population growth. In the case of summer predation, the interaction was strongest at moderate to heavy levels of predation (Fig. 2, center right). When predation rates in both seasons were varied together, reproductive pauses had the greatest effect on the response surface at moderate levels of predation (Fig. 2, bottom right). These departures from growth rates expected under the null models were directly related to the magnitude of the mortality trade-offs. Increasing the effect of a calf on adult female mortality had its greatest effect on the interaction with summer predation, whereas increasing the effect of maternal care on

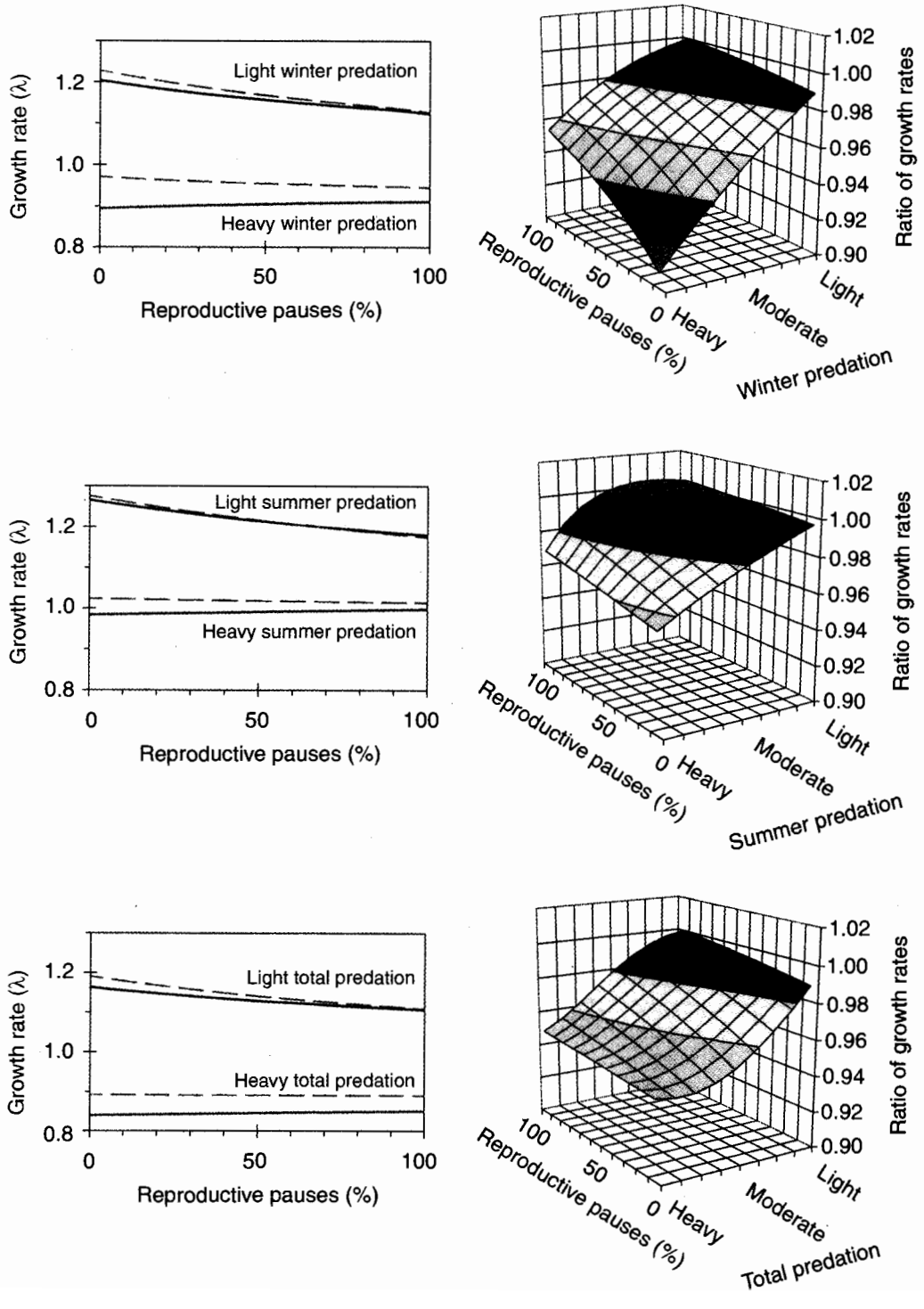
→

FIG. 2. Comparisons of population growth rate (λ) with varying bottom-up costs of reproduction and the presence or absence of various top-down costs of reproduction. The model (Table 1) employed a simplified life history of three age classes (calf, yearling, adult) and maximum reproduction by adults (1 calf) beginning at age 2. Bottom-up costs of reproduction were modeled by increasing the proportion of nursing females (3 mo of lactation) that skipped reproduction the following year (percentage reproductive pauses). Top-down (predation) impact was modeled as occurring primarily in winter (top), summer (middle), and both seasons (bottom) with the mortality rates varied across the ranges given in Table 2. Models with top-down life history trade-offs (solid lines in left column) included a higher rate of mortality of adults when accompanied by a calf, and a lower rate of yearling mortality if the adult remained with her yearling. The null models (broken lines) assumed low yearling and high adult survival (see *Methods*). The right column shows the response surfaces for ratios of population growth rate that incorporated top-down life history trade-offs to those that did not (λ_T:λ_N), as a function of bottom-up trade-offs (percentage reproductive pauses) after lactation and severity of predation in winter (top), summer (middle), and in both seasons (bottom). Shading provides perspective relative to the vertical axis.

yearling survival increased the interactions with both summer and winter predation.

Discussion

Assuming that either bottom-up or top-down mechanisms excise a cost of reproduction to females, that cost would reduce average reproductive or survival rates, respectively. Without their interaction at the individual level, the effect of reducing average survival or reproduction is simply a higher rate of population decline. However, the interaction of bottom-up and top-down life history trade-offs was mildly antiregulatory



in the models. In other words, a moose population able to increase under chronically high predation could reach a point where increasing nutritional constraints actually increase the recruitment and survival of adults as a consequence of declining calf production, and sustain higher than expected growth rates. Where predation is driving a decline in the prey population, one might expect (1) density-dependent constraints on reproductive trade-offs to lessen, and (2) predation impact to increase as the ratio of predators to prey increases, thereby moving the prey population directly down slope on the response surfaces of Fig. 2 and accentuating the decline. The simulated interactions should be most relevant to the range of densities where nutritional constraints change most rapidly; for example, near carrying capacity (K) or at relatively high densities (McCullough 1984, Fowler 1987), and where predator numbers (e.g., brown bears) respond slowly to changing moose abundance. Thus, the effects of life history interactions could be antiregulatory and potentially destabilizing to predator–prey interactions, particularly around potential equilibria at high prey densities (Gasaway et al. 1983, Messier 1994). The effect of such an interaction relative to more direct ecological effects on survival and reproductive parameters (e.g., Fig. 2) appears small, but because of the antiregulatory nature of the change, subtle effects on the stability of predator–prey interactions cannot be excluded. Also, the magnitude of mortality trade-offs simulated here were based on those observed at a single study site (Testa 2004); mortality trade-offs of greater magnitude would magnify this effect.

While the general models (Fig. 2) suggest that both wolves and bears could produce life history interactions that affect population growth, such trade-offs were greatest in summer for moose in south-central Alaska being preyed upon primarily by bears (Testa 2004). Thus, it is possible that in addition to the predation load added by bears to wolf–moose models, life history interactions involving bear predation could contribute to instability of potential equilibria of moose–predator interactions at high moose densities (Gasaway et al. 1992, Messier 1994, Ballard and Van Ballenberghe 1998).

A critical caveat to this discussion is that the modeling approach used here did not explicitly incorporate the underlying differences in prey vulnerability, which are only implied by the observed differences in mortality. The interaction of life history trade-offs in these models reflects the changing composition of the population under different assumptions, but does not explicitly alter the underlying vulnerability to predators or possible dynamic responses by the predators. I limited the approach in this way because the importance of variable prey vulnerability in predator–prey interactions is so poorly known. Common theoretical treatments of predator–prey dynamics (e.g., Keith 1983, Arditi and Ginzburg 1989, Messier 1994, Eberhardt and Peterson 1999, Hayes and Harestad 2000) ignore well-known differences in vulnerability to predation between adults and juveniles, and between mature and senescent adults (Peterson 1977, Peterson et al. 1984, Ballard et al. 1991). The implications of life history interactions to predator–prey theory need to be explored in this larger context of class-specific vulnerability, where varying vulnerability and composition of the prey are likely to have strong effects on both the functional and numeric response of predators and feedback to the prey population.

Facultative reduction of reproductive effort in the presence of high predation risk has been supported by models and experimental evidence as an effective strategy to maximize reproductive success (Dehn 1994, Oksanen and Lundberg 1995, Kokko and Ruxton 2000). However, the models used here make no assumption that the observed trade-offs represent optimal strategies at the individual level, only that they reflect phenotypic trade-offs observed in moose (Testa 2004). The model of life history interactions in Alaskan moose (Fig. 1) could be interpreted as a fitness model for individual reproductive strategies under the observed predation pressure, predicting a weak optimum (highest value of λ) of obligatory reproductive pauses following reproduction when top-down trade-offs are important. That reproductive pauses are the exception rather than the rule suggests that moose were not exercising an optimal strategy under the conditions in that study (Testa 2004). Moose may lack a physiological mechanism for breeding suppression in response to predators (Dehn 1994, Kokko and Ruxton 2000). The ability to recognize when bottom-up or top-down factors will have the greater effect on reproductive success may be difficult for individual moose, particularly if the temporal and spatial scales of change in either relationship are shorter than those encountered by moose during two reproductive cycles. Wolf numbers can increase dramatically in a single year (Keith 1983, Peterson et al. 1984, Ballard et al. 1987) and snow conditions can alter the nutritional environment unpredictably within a single reproductive cycle. Similarly, movements of moose in a few days can alter their exposure to deep snow and risk of predation, as well as forage availability. If the pattern and magnitude of predation risks are less predictable than the nutritional conditions affecting individual moose, nutritional constraints on reproductive effort would be expected to take precedence over perceived risk of predation.

Acknowledgments

I am indebted to Don Spalinger, Don Siniff, Joel Berger, and four anonymous reviewers for constructive critiques. This work was supported by Federal Aid in Wildlife Restoration Project W-27-1 and the Alaska Department of Fish and Game.

Literature Cited

Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator–prey dynamics: ratio-dependence. Journal of Theoretical Biology **139**:311–326.

Ballard, W. B., and V. Van Ballenberghe. 1998. Predator/prey relationships. Pages 247–273 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs **98**:1–51.

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs **114**:1–49.

Berryman, A. A., J. Michalski, A. P. Gutierrez, and R. Arditi. 1995. Logistic theory of food web dynamics. Ecology **76**: 336–343.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. Nature **337**:260–262.

Dehn, M. M. 1994. Optimal reproduction under predation risk: consequences for life history and population dynamics in microtine rodents. Dissertation. Simon Fraser University, Burnaby, British Columbia, Canada.

Eberhardt, L. L., and R. O. Peterson. 1999. Predicting the wolf–prey equilibrium point. Canadian Journal of Zoology **77**:494–498.

Fowler, C. W. 1987. A review of density dependence in populations of large mammals. Pages 401–441 *in* H. H. Genoways, editor. Current mammalogy. Plenum, New York, New York, USA.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs **120**:1–59.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs **84**:1–50.

Gutierrez, A. P., N. J. Mills, S. J. Schreiber, and C. K. Ellis. 1994. A physiologically based tritrophic perspective on bottom-up-top-down regulation of populations. Ecology **75**:2227–2242.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.

Hayes, R. D., R. Farnell, R. M. P. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildlife Monographs **152**:1–35.

Hayes, R. D., and A. S. Harestad. 2000. Wolf functional response and regulation of moose in the Yukon. Canadian Journal of Zoology **78**:60–66.

Keith, L. B. 1983. Population dynamics of wolves. Pages 66–77 *in* L. N. Carbyn, editor. Wolves in Canada and Alaska: their status, biology and management. Alta, Edmonton, Alberta, Canada.

Kokko, H., and G. D. Ruxton. 2000. Breeding suppression and predator–prey dynamics. Ecology **81**:252–260.

McCullough, D. R. 1979. The George Reserve deer herd. University of Michigan Press, Ann Arbor, Michigan, USA.

McCullough, D. R. 1984. Lessons from the George Reserve, Michigan. Pages 211–242 *in* U. K. Halls, editor. White-tailed deer ecology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology **75**: 478–488.

Messier, F., J. Huot, D. Le Henaff, and S. Luttich. 1988. The demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic **41**:279–287.

Oksanen, L., and P. Lundberg. 1995. Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. Evolutionary Ecology **9**:45–56.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Government Printing Office, Washington, D.C., USA.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs **88**:1–52.

Sinclair, A. R. E., C. J. Krebs, J. M. Fryxell, R. Turkington, S. Boutin, R. Boonstra, P. Seccombe-Hette, P. Lundberg, and L. Oksanen. 2000. Testing hypotheses of trophic level interactions: a boreal forest ecosystem. Oikos **89**:313–328.

Testa, J. W. 1987. Long term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Canadian Journal of Zoology **65**: 2993–2997.

Testa, J. W. 1996. Using annual approximations for birth rate in models for species with multiannual reproductive cycles. Marine Mammal Science **12**:428–433.

Testa, J. W. 1998. Compensatory response to changes in calf survivorship: management consequences of a reproductive cost in moose. Alces **34**:107–115.

Testa, J. W. 2004. Population dynamics and life history trade-offs of moose (*Alces alces*) in south-central Alaska. Ecology **85**:1439–1452.

Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy **79**:1345–1354.

Testa, J. W., E. F. Becker, and G. R. Lee. 2000. Temporal patterns in the survival of twin and single moose calves (*Alces alces*) in southcentral Alaska. Journal of Mammalogy **81**:162–168.