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Mass-Balance Analyses of Boreal Forest Population Cycles: Merging Demographic and Ecosystem Approaches

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Abstract

Using Ecopath, a trophic mass-balance modeling framework, we developed six models of a Canadian boreal forest food web centered around snowshoe hares, which have conspicuous 10-year population cycles. Detailed models of four phases of the cycle were parameterized with long-term population data for 12 vertebrate taxa. We also developed five other models that, instead of observed data, used parameter values derived from standard assumptions. Specifically, in the basic model, production was assumed to equal adult mortality, feeding rates were assumed to be allometric, and biomass was assumed to be constant. In the actual production, functional response, and biomass change models, each of these assumed values from the basic model was replaced individually by field data. Finally, constant biomass models included actual production by all species and functional responses of mammalian predators and revealed the proportion of herbivore production used by species at higher trophic levels. By comparing these models, we show that detailed information on densities and demographics was crucial to constructing models that captured dynamic aspects of the food web. These detailed models reinforced an emerging picture of the causes and consequences of the snowshoe hare cycle. The snowshoe hare decline and low phases were coincident with times when per capita production was relatively low and predation pressure high. At these times, ecotrophic efficiencies (EE) suggest there was little production that remained unconsumed by predators. The importance of both production and consumption implies that bottom–up and top–down factors interacted to cause the cycle. EEs of other herbivores (ground squirrels, red squirrels, small mammals, small birds, grouse) were generally low, suggesting weak top–down effects. Predation rates on these "alternative" prey, except ground squirrels, were highest when predators were abundant, not when hares were rare; consequently, any top–down effects reflected predator biomass and were not a function of diet composition or functional responses. Finally, several predators (lynx, coyotes, great-horned owls) showed clear bottom–up regulation, reproducing only when prey exceeded threshold densities. Taken altogether, these results demonstrate that ecosystem models parameterized by population data can describe the dynamics of nonequilibrial systems, but only when detailed information is available for the species modeled.

Key words: snowshoe hare; boreal forest; lynx; arctic ground squirrel; red squirrel; Ecopath; mass-balance models; food web.

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INTRODUCTION

Because of their opposing foci on energy flow and population abundances, respectively, ecosystem and population approaches have traditionally been viewed as alternative strategies for understanding ecological systems (O'Neill and others 1986). Although linking the two represents a challenge (Hairston and Hairston 1993; Jones and Lawton 1995), it may provide insight into the structure and function of complex multispecies assemblages. As a basic currency of life, energy can be transferred among organisms or dissipated but is never created de novo. Available energy and the efficiency of transfer thus set bounds to the interaction webs that can persist. Conversely, the rates at which energy can be consumed and transferred into new production are affected by population parameters, including life histories and the body sizes of taxa (Peters 1983; Nagy 1987; Yodzis and Innes 1992).

In this paper, we develop ecosystem models based on population-level data to analyze a dramatic ecological phenomenon: the 10-year population cycle of snowshoe hares (*Lepus americanus*) and their predators that occurs across Canada and Alaska (Keith 1990; Krebs and others 1995; Stenseth and others 1999; Hodges 2000). Extensive population-level data from the Kluane boreal forest ecosystem (Krebs and others 2001b) allow us to parameterize energy-flow models using various assumptions about production, consumption, and steady states. We use these parameterizations, along with calculated values of ecological efficiencies, to gain insight into causes of vertebrate food web dynamics. As an added benefit, we explore the important issue of how much and what kind of data are needed to parameterize an ecosystem model without making major biological blunders.

We use a mass–balance modeling system, Ecopath, that has been used primarily to describe fish-centered aquatic food webs (Christensen and Pauly 1992, 1993). The Ecopath master equation is:

$$B_r \cdot \left(\frac{P_r}{B_r}\right) \cdot \mathrm{EE}_r = \sum_{\text{all } c}\left[(B_c) \cdot \left(\frac{Q_c}{B_c}\right) \cdot (d_{rc})\right] + \Delta B_r \tag{1}$$

where B is biomass, P is net production, Q is consumption (ingestion), with subscripts referring to resource (r) and consumer (c) taxa. The proportion of r in the diet of c is d_{rc}. At equilibrium, $\Delta B_r = 0$. A taxon's ecotrophic efficiency (EE) is the ratio of how much of that taxon is consumed by higher trophic level species relative to the taxon's net production. Ecotrophic efficiency thus parallels earlier concepts of utilization efficiency or the ecotrophic coefficient (Kozlovsky 1968). Unconsumed production becomes detritus, for instance via disease, injury, starvation-induced mortality, or uneaten kills. Biomass accumulation and emigration (ΔB greater than 0) raise the value of EE calculated in Ecopath. The aquatic ecosystems commonly modeled in Ecopath are generally assumed to be at equilibrium (ΔB equals 0) for a given period, during which the transfer of biomass among portions of the food web is assumed not to alter standing stocks. Production and consumption rates are generally also modeled as invariant. Production (P/B) is often based on adult mortality, because production must match mortality if a closed population is equilibrial (Allen 1971). Consumption (Q/B) is often based on allometric relationships between body size and metabolic rate (Peters 1983).

Common assumptions about steady-state values of biomass, production, and consumption do not hold for the boreal forest food web. We know a priori that there are dramatic changes in standing biomass because of the pronounced cyclicity. Furthermore, research on this food web has demonstrated cyclic changes in productivity (reproduction and growth) and consumption (numeric and functional responses of predators) (Keith 1990; O'Donoghue and Krebs 1992; Krebs and others 1995; Rohner 1996; Slough and Mowat 1996; O'Donoghue and others 1997, 1998b; Stefan 1998; Karels and others 2000). Appropriate parameterization of Ecopath models for the boreal forest food web may therefore require considerably more complex models than are acceptable for systems that are closer to equilibrium. When EE is greater than 1, models are unbalanced because there is not enough production to account for all of the known fates of a species' biomass. However, because of our focus on modeling nonequilibrial dynamics, we never attempt to "balance" the biomass flows in our models, instead relying on inequalities to compare parameterization methods and ecological processes governing different phases of the cycle.

The use of energy-flow models to understand community dynamics has met with considerable skepticism because there is no strict correlation between energy flow and trophic impact (Paine 1980; Polis 1994). Here, however, we do not focus on the magnitude of transfers, but on the efficiencies, which have direct relevance for understanding top–down and bottom–up effects in this cyclic system. Ecotrophic efficiencies indicate the strength of top–down interactions, especially if EE primarily reflects consumption. Specifically, for EE approximately equal to 1 in a steady-state system, all production is

Table 1. Six Parameterizations for Ecopath Models of the Kluane Boreal Forest Ecosystem

	$\Delta B = 0$		ΔB = empirical	
	P/B = adult mortality	P/B = empirical	P/B = adult mortality	P/B = empirical
Q/B = allometric	Basic	Actual production	Biomass change	
Q/B = empirical	Functional response	Constant biomass		Detailed

used by consumers, indicating that consumers can affect the standing stock of the resource. Alternatively, if EE is much less than 1, consumers simply skim off a bit of excess production without exerting a top–down effect. The rate at which a resource is consumed relative to its production rate alters the strength of the interaction between species (Ruesink 1998). Additionally, trophic structure itself may influence energy flow. A trophic level limited by consumers may be maintained at such low abundance that the trophic level below is hardly utilized, potentially yielding low EEs in component taxa (Hairston and others 1960; Oksanen and others 1981; Hairston and Hairston 1993). Indeed, a great deal of discussion has addressed whether strong top–down effects are common at the level of entire trophic levels. Some suggest, for instance, that trophic cascades should be uncommon except in aquatic systems (Strong 1992; Polis 1994, 1999). Yet arctic and boreal terrestrial ecosystems include several examples of strong top–down interactions between predators and prey or herbivores and plants (Oksanen and Oksanen 2000). Using Ecopath to assess ecological efficiencies of particular taxa in the Kluane boreal forest food web, we achieve a new understanding of interaction strengths and how they vary through the cycle.

Gross conversion efficiency (GE) may be similarly useful for insight into bottom–up effects in food webs. GE is the ratio of net production to consumption (P/Q) within a single taxon and addresses how well a taxon can convert biomass ingested into reproduction and growth. The difference is either unassimilated or used for maintenance metabolism. GE is thus similar to earlier concepts of ecological growth efficiency or gross efficiency of growth (Kozlovsky 1968). If GE is constant, then any increases in consumption translate into increased net production, a bottom–up effect. If GE equals 0 below a threshold of food supplies, then increased resource abundance will increase net production only after the threshold is exceeded. No bottom–up effect occurs when changes in consumption do not affect net production.

Our primary goal in this paper is to evaluate the trophic dynamics in the boreal forest food web, specifically to assess the top–down versus bottom–up nature of the dynamics during the snowshoe hare cycle. Model development and interpretation are potentially affected by parameterization at two levels: How are parameter values calculated? And within each method of parameterization, how well are parameter values known in light of uncertainty in field data? We address the biological and modeling issues simultaneously by contrasting results from models constructed using increasingly realistic parameterizations (Table 1) and by evaluating the effects of uncertainty on model outputs. In this fashion, we can evaluate the level of biological detail required to capture the behavior of this dynamic ecosystem and the degree of confidence we can place on model outputs, given uncertainty in data inputs.

Methods

Study System

The cyclic system we modeled is that of the well-known snowshoe hare–Canadian lynx (*Lynx canadensis*) cycle (Keith 1963; Krebs and others 1995). We used data from the Kluane Boreal Forest Ecosystem Project, which is situated in the boreal forest in southwest Yukon Territory, Canada (Krebs and others 1995, 2001b; Boutin and others 1995). Snowshoe hares at Kluane have cyclic dynamics that are typical of fluctuations throughout the boreal forest of North America (Hodges 2000). During the 1988–97 cycle, spring hare densities varied approximately 18-fold at Kluane (Hodges and others 2001). We focus on four phases of the hare cycle, always considered from one autumn to the next: peak phase (1988–89), decline (1990–91), low (1992–93) and increase (1994–95). These phases are based on hare densities; some of the other cyclic species were 1–2 years out of phase with the hares (Boutin and others 1995; Krebs and others 2001b). In all cases except for the cyclic peak, these years represent the 1st year of a multiyear phase (Figure 1).

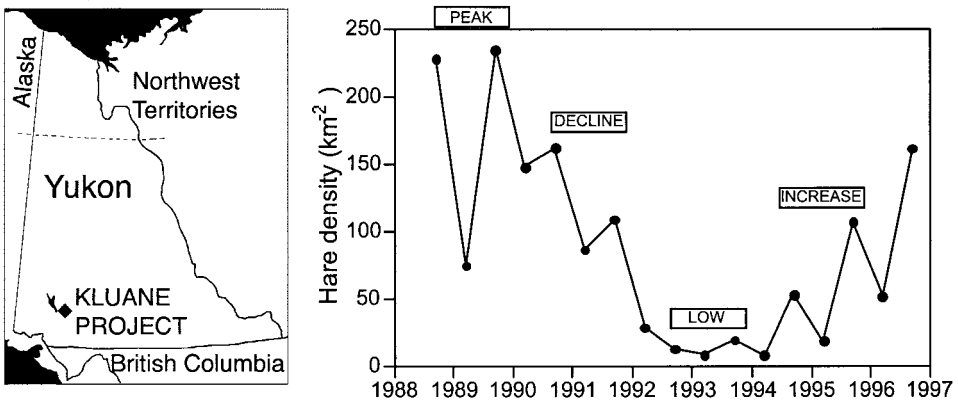
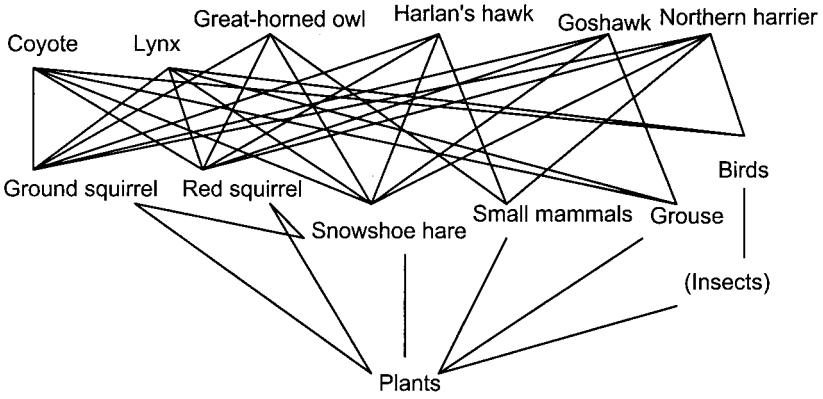


Figure 1. Study site, food web, and conspicuous cyclic dynamics in the Kluane boreal forest ecosystem. Many small birds are insectivores, but we connected this taxon directly to primary producers because we were unconcerned with the details of lower trophic level dynamics. Boxes superimposed on the time series of hare densities show periods explored with annual models.



The Kluane Project research was conducted in the boreal forest of the Shakwak Trench (60°57′N, 138°12′W), a broad glacial valley that runs east from the southern end of Kluane Lake, Yukon, Canada (Figure 1). To the north and south are the mountains of the Ruby and Kluane Ranges, respectively, while the valley itself averages 900 m above sea level. The dominant forest tree is white spruce (*Picea glauca*) with patches of balsam poplar (*Populus balsamifera*) and aspen (*P. tremuloides*) and a 0.5–2-m–tall shrub layer of birch (*Betula glandulosa*), willow (*Salix* spp.), and soapberry (*Shepherdia canadensis*).

Figure 1 depicts the trophic relationships among the most common vertebrate taxa in the Kluane food web, which we used for the models in this paper. A more detailed food web is given in Krebs and others (2001b). We modeled the vertebrates in some detail, but we did not explicitly model plants or insects. We also ignored a number of small predators (mustelids, foxes) and large mammals (moose, grizzly bear, wolves) that are relatively uncommon and were unstudied at Kluane. From 1988 to 1997, experimental manipulations (fertilization, herbivore exclusion, food addition, predator exclusion) were conducted to evaluate the interactions of the different trophic levels (Krebs and others 1995, 2001b; Turkington and others 1998; Sinclair and others 2000). In this paper, however, we use data collected from control areas because we wish to address the dynamics of the unmanipulated system (see Ruesink and Hodges 2001 for Ecopath analyses of treatment effects). Whenever possible, we used published demographic and trophic information from the Kluane boreal forest ecosystem. We also used data from other boreal research papers or from the unpublished data of individual researchers at Kluane as needed to supplement the published Kluane material.

Our models addressed food web dynamics for the Kluane ecosystem as a whole, although particular species were studied at different locations within the Shakwak Trench. For prey species, densities were sampled from sites throughout the valley (Folkard and Smith 1995; Karels and others 2000; Martin and others 2001; Boonstra and others

2001a, 2001b; Hodges and others 2001), and we averaged values from the different sites. Sampling sites ranged in area from 2.8 ha (mice and voles) to 60 ha (hares and grouse). For raptors, densities were assessed in a 100 km^2 intensive study area, and these densities were extrapolated to the entire area (Doyle and Smith 1994, 2001; Rohner 1996; Rohner and others 2001). For the mammalian predators, density estimates were made on a valley-wide basis—that is, 400 km^2 (O'Donoghue and others 1997, 2001).

Ecopath Modeling Framework

We constructed mass-balance models of the Kluane food web using Ecopath. Ecopath is based on the mass-balance models of Polovina (1984) and is a Windows-based software program developed at the International Centre for Living Aquatic Resources Management (www.ecopath.org), (Christensen and Pauly 1992, 1993). We parameterized six separate Ecopath models for each of the four phases of the cycle (Table 1). Basic models were modeled with equilibrial assumptions: no biomass change (ΔB equals 0), production (P/B) equivalent to adult mortality, and consumption (Q/B) based on allometric energy requirements. This parameterization method most closely approximates the common strategy used in aquatic Ecopath models (Okey and Pauly 1998). We created five other model types—three models relaxing one assumption each, one relaxing two, and one model relaxing all three assumptions simultaneously. In biomass change models, we explicitly modeled the observed changes in biomass (ΔB) of cyclic species. To relax the assumption of equilibrial production equaling adult mortality, we constructed actual production models for which P/B was based on observed reproduction and growth. In functional response models, we based Q/B on the empirically observed kill rate data of mammalian predators rather than on allometric requirements. Constant biomass models included actual production and predator functional responses. Finally, we constructed detailed models that incorporate all three of these elaborations on the basic models. Using different parameterizations allows us to ask questions such as: Do functional responses of predators contribute to hare population declines? (basic versus functional response); What proportion of net production is ingested (or at least killed) by higher trophic levels? (constant biomass); and What is the role of variable production in driving cyclic density changes? (basic versus actual production). The details of how we extracted Ecopath parameters from population-level data follow.

Biomass

For vertebrates, we had estimates of density and individual body mass; their products provide estimates of biomass per area. Snowshoe hares and ground squirrels were modeled with ΔB not equal to 0 because individual biomass and population size varied over time (Karels and others 2000; Hodges and others 2001). Cyclic mammalian and avian predators were modeled with ΔB not equal to 0 because population sizes varied (Doyle and Smith 1994, 2001; Rohner 1996; O'Donoghue and others 1997; Rohner and others 2001). For hares and ground squirrels, we used both fall and spring population estimates, and we incorporated the variation in body mass estimates that occurred during the cycle. Ground squirrels were trapped using one regime prior to 1991 and another thereafter; we apply spring 1991 densities to previous years because of the noncomparability of the trapping estimates from the two periods (T. Karels personal communication). For all other taxa, we modeled body mass as constant through time because the natural variation was not cyclic and the variation was small (Krebs and Wingate 1985; Boonstra and others 2001b; Martin and others 2001). Red squirrel densities remained fairly constant from year to year, but fall densities always exceeded spring densities, so we calculated an average fall and an average spring density using data from all years (S. Boutin and others unpublished; Boonstra and others 2001a).

For lynx and coyotes, densities were estimated over winter (O'Donoghue and others 1997). Raptors (great-horned owls, goshawks) were surveyed in spring (F. I. Doyle unpublished; Doyle and Smith 2001; Rohner and others 2001). For all remaining vertebrate taxa (grouse, small mammals, small birds) we calculated average densities based on all available density estimates from fall 1988 to spring 1996 inclusive (Folkard and Smith 1995; Boonstra and others unpublished 2001b; Martin and others 2001). The densities of these taxa either had small coefficients of variation through time, and/or the fluctuations in their densities varied randomly with respect to the hare population cycle. Eight species of small birds contributed to that taxon (Folkard and Smith 1995). Their densities, weighted by body size, were increased 10% to account for other, rarely detected species. The small mammal taxon combined values for *Microtus* and *Clethrionomys* spp. (Boonstra and others 2001b).

Consumption per Biomass (*Q/B*)

We used the allometric relationships between body mass and consumption rates derived by Nagy (1987) to estimate the daily energy needs of the various taxa. These relationships were calculated independently for birds, mammalian herbivores, and mammalian predators. These energy estimates were derived from field data and represent average energy needs of active animals. We calculated energy needs as kcal kg^{-1} y^{-1}. The biomass necessary to meet these energy needs depends on the energy content of the food and the efficiency of energy assimilation by the consumer. We assumed an assimilation efficiency of 80% (Parks 1982). We assumed the energy content of plants to be 1 kcal/g and of animals to be 1.75 kcal/g fresh weight (FW) (Parks 1982). This estimate of 1.75 kcal/g for animals has been empirically confirmed for snowshoe hares. Captive coyotes obtained 1.4 kcal/g FW of metabolizable energy from snowshoe hares (Litvaitis and Mautz 1980), which is equivalent to 80% of 1.75 kcal/g. To account for migration and hibernation, we multiplied feeding rates of ground squirrels and migratory avian predators and songbirds by one-third because these species are active at Kluane for only 4 months of the year.

These allometric estimates of consumption matched independent field data (Pease and others 1979; Hodges 1998) and expert opinions on feeding rates of hares and avian predators at Kluane (K. Hodges unpublished; F. I. Doyle personal communication). Lynx and coyotes, however, killed hares in excess of their allometric estimate during the cyclic peak, but they killed hares at lower rates during the low phase (O'Donoghue and others 1998b). Thus, for mammalian predators we calculated separate feeding rates for each phase of the cycle using direct estimates of annual predation rates on hares, weighted by the proportion of hares in the biomass of the diet (O'Donoghue and others 1998a, 1998b).

Diet Composition

The diets of lynx and coyotes were estimated from the analysis of prey remains in scats (O'Donoghue and others 1998b). We weighted winter scats by two-thirds and summer scats by one-third to relate these diets to the seasons at Kluane. The diets of goshawks, Harlan's hawks, and northern harriers were estimated from prey remains occurring at nests in the summer (Doyle and Smith 2001). We assumed that the adults provisioned young with food similar to their own diets. Diets of great-horned owls were estimated from pellet remains and prey remains at nests (Rohner 1994; Rohner and others 2001). Most of the owl diet data were obtained from summer estimates; we weighted both summer and winter as half the diet for owls to reduce the contribution of limited winter data. During winter, about 90% of their diet consists of hares (Rohner 1996), and we assumed the remainder was half small mammal and half red squirrel. Prey remains indicate the number of individuals killed; to convert to biomass, we multiplied individuals by the average body mass of each prey type. We used masses of 0.1 and 0.7 kg for leverets (less than 30 days old) and juvenile hares (less than 6 months old), respectively.

Many snowshoe hare leverets were killed by red squirrels and ground squirrels (O'Donoghue 1994; Stefan 1998; Hodges and others 2001). To calculate the proportion of each squirrel species' diet composed of leverets, we calculated kg hares consumed per kg squirrel per year:

$$q_{Lp} = \frac{L \cdot (1-S_L) \cdot m_{Lp} \cdot b_L}{B_p} \qquad (2)$$

where q_{Lp} is consumption of leverets by squirrels, L is the number of leverets born, S_L is leveret survival rate to 30 days based on data from radiotagged leverets, m_{Lp} is the proportion of leveret mortality due to squirrels, b_L is the average mass of a single leveret (0.1 kg), and B_p is total squirrel biomass. Snowshoe hare production and mortality parameters were taken from Stefan (1998), O'Donoghue (1994) and O'Donoghue and Krebs (1992); squirrel biomass estimates were derived from population estimates as shown above. We calculated squirrel consumption of leverets separately for ground squirrels and red squirrels. For each species, we then determined what proportion of their total (allometric) consumption consisted of hares. In fact, this calculation may overestimate the contribution of hares to squirrel diet, if portions (that is, more than 20% unassimilated) of carcasses remain unconsumed.

Production per Biomass (*P/B*)

For three models (basic, biomass change, functional response), we used the common parameterization technique of assuming that production per biomass (*P/B*) equals the adult mortality rate. We had estimates of mortality for most species (Table 2). For actual production, constant biomass, and detailed models, we calculated *P/B* using reproduction, growth, and recruitment data. Unlike most Ecopath models, which use annual production divided by average annual biomass, we used initial fall biomass

Table 2. Annual Survival Calculations Used for Production/Biomass values (P/B = adult mortality = 1–survival) in Basic, Functional Response, and Biomass Change Models

	Adult Survival Interval	Years Available	Annual Survival Calculation	Survival Values for Four Phases of Cycle
Hares	Annual Apr–Mar (s_a)	1988–96	$(s_a + s_{a+1})/2$	0.25, 0.07, 0.10, 0.25
Ground squirrels	28-d active season (s_{28}) Overwinter (s_o)	1990–96	$\exp^{(4 \ln(s_{28}))} (s_o)$	0.32[a], 0.33, 0.15, 0.39
Red squirrels	Mar–Aug (s_s) Sept–Feb (s_o)	1988–96	(s_s) (s_o)	0.81, 0.58, 0.62, 0.50
Lynx	30-wk overwinter	1988–96	Use directly[c]	0.75, 0.69, 0.06, 1.0
Great-horned owl	Annual fall–fall	1989–92	Use directly	0.93, 0.96, 0.60, 0.60[b]

Four phases correspond to hare peak (1988–89), decline (1990–91), low (1992–93), and increase (1994–95).
[a]*Ground squirrel survival at the peak was unavailable for 1988–89, so average values from the other three model years were used.*
[b]*Great-horned owl survival was available only for 1990–91 (0.97) and 1991–92 (0.60). We took these as representative of times when hares were common vs rare.*
[c]*Overestimates survival.*

for our denominator so that we could explicitly address biomass change during the year. Similarly, our estimates of production were based on animals that were present in the spring. If separate fall and spring estimates were not available, as was the case for most predators, breeding densities were assumed to equal fall densities.

For both raptors and mammalian predators, we calculated production as the recruitment (R) of young into the adult population (with units of individuals/individual/y or kg/kg/y). This calculation does not incorporate the "production" of growing offspring that died before adulthood, because we have no data for these individuals. In terms of parameterization, therefore, R is less than or equal to actual production. For raptors,

$$R = r \cdot f \cdot n \tag{3}$$

and for lynx,

$$R = r \cdot (A \cdot f_a \cdot n_a \cdot s_a + Y \cdot f_y \cdot n_y \cdot s_y) \tag{4}$$

where r is the proportion of adult females, f is the proportion of females breeding, n is litter size or young fledged, and s is survival until maturity. For lynx, yearling females differed from adult females in their reproductive parameters (Slough and Mowat 1996). We therefore calculated reproduction for each group separately, with A and Y representing the proportion of females in each age class and subscripts denoting age-specific parameters. We assumed that raptors fledged at adult mass, so there was no need to include a survival term. We were unable to locate any information on coyote reproduction in the boreal forest, so we modeled coyote production as identical to lynx production: The temporal patterns in hunting group sizes of lynx and coyotes (an index of reproduction) at Kluane were similar (O'Donoghue and others 1997). We calculated production by small mammals (6.6 y^{-1}) and grouse (2.2 y^{-1}) using similar equations. For small birds, we set P/B equal to 2 y^{-1} because fledging rates should at least equal those of larger avian species. Also, fledging rates for warblers in Hubbard Brook deciduous forest had median values of 3 or 4 per pair (Rodenhouse and Holmes 1992), close to $P/B = 2\ y^{-1}$.

For the remaining taxa, data were available on the growth rates and survival of the young, thus allowing us to include the biomass of young that did not reach adulthood in our estimates of production. For ground squirrels and red squirrels, production (P) was calculated from emergence from the nest (when offspring first become vulnerable to predation) to adulthood, using the following equation:

$$P = d \cdot r \cdot f \cdot n \cdot \left(b + \int_{t=0}^{t_j} g \cdot e^{mt} \right) \tag{5}$$

where d is the breeding density, r is the proportion of females in the breeding population, f is the proportion of females breeding, n is litter size, b is individual offspring mass at emergence, g is the daily growth rate of young, m is the daily exponential mortality rate (m less than 0), and t is the time at which animals leave the juvenile stage, calculated from the difference between emergence and adult weights divided by growth rate. To obtain production per biomass, this production was di-

vided by fall biomass. For ground squirrels, we used year-specific data for all parameters except size of emerging young (for which only 1993 data were available) and growth rate (which appears to remain constant) (T. Karels personal communication). We used year-specific birth, growth, and survival data for red squirrels, although population densities were kept constant because interannual variation in density was low.

For hares, mortality rates of leverets differed from those of juveniles, which required that we distinguish the production accruing from each stage. Specifically:

$$P = d \cdot r \cdot \sum_{L=1}^{4} f_L \cdot n_L \cdot \left(b_L + \int_{t=0}^{t_1} g_L \cdot e^{m_L \cdot t_1} + \int_{t=t_1}^{t_2} g_j \cdot e^{m_j \cdot t_2} \right) \tag{6}$$

Variables are the same as in the production equation for squirrels, with L referring to the litter group—that is, b_L, g_L, and m_L (less than 0) refer to the birth weight, growth rate, and daily mortality rate per litter group. Juvenile parameters for growth (g_j) and daily mortality rate (m_j less than 0) were assumed constant for all litter groups. We had juvenile survival data only for the increase year of 1995–96 (Gillis 1998), so these values were applied to all years, whereas we used year-specific leveret parameters (O'Donoghue and Krebs 1992; O'Donoghue 1994; Stefan 1998). The time units t_1 and t_2 represent days to the end of the leveret and juvenile phases, respectively, and were calculated based on the length of time it would take for an individual to grow to the next phase (that is, for leverets to reach 0.5 kg and for juveniles to reach adult weight), given known initial biomass and growth rate. The growth rate of leverets differed slightly among litter groups 1 and 2, and growth rates of leverets in litters 3 and 4 were assumed to be intermediate (O'Donoghue and Krebs 1992).

Although the vertebrate food web is fueled by primary productivity of plants, we did not model plant production explicitly. In a separate paper, we have shown that sufficient plant biomass exists at Kluane to support energetic requirements of herbivores, even at the peak of the hare cycle (Ruesink and Hodges 2001; Sinclair and others 2001). Our calculations of available plant biomass exclude inedible tissues such as tree trunks but do not otherwise address issues of food quality. If plant nutritional quality were low, herbivores could experience food limitation despite high plant biomass. For example, dietary protein content affects hare body mass and starvation rates (Sinclair and others 1982; Rodgers and Sinclair 1997). The trophic manipulations at Kluane have also shown that food supply and predation pressure interact in their effects on snowshoe hare population dynamics, possibly resulting from foraging changes by hares in response to predation risk (Krebs and others 1995, 2001a).

Modeling Uncertainty in Snowshoe Hare Parameters

Ecopath was used to generate ecotrophic efficiencies (EE) and gross conversion efficiencies (GE) for vertebrates in the Kluane food web (Figure 1) for four phases of the cycle and for six of eight possible methods of parameterization (Table 1). In all cases, we parameterized Ecopath using mean values. Consequently, the models provide no indication of the certainty of the estimates of energy flow through the Kluane food web. For snowshoe hares only, we carried out separate calculations for EE that incorporated variation in parameter values. Specifically, we calculated EE repeatedly in a Monte Carlo simulation in an Excel spreadsheet (Excel 2000; Microsoft, Redmond, WA, USA). We based simulations on Eqs. (1) and (6), assuming that ΔB equals 0, which is equivalent to the constant biomass Ecopath model. For each simulation run, we drew values for each parameter randomly from its probability density function. Mean values, variation, and distribution type for each parameter are provided in Table 3.

Densities, feeding rates, and the diet composition of predators at Kluane are point estimates without estimates of uncertainty. Therefore, de facto, our explorations of uncertainty in snowshoe hare EE derive exclusively from variation in parameters associated with hare production. Variation in hare EE would probably be larger if consumption parameters derived from predation data also had associated error estimates. For example, Nagy's (1987) estimates of field metabolic rates have confidence limits of −58% to +138%, which could increase estimates of losses to predators, and therefore EE, over twofold.

In translating parameter values for hare production into Monte Carlo simulations, three problems arise. First, two ways of estimating variation in hare density are possible. Each grid had variation associated with its mean value based on mark-recapture techniques (Krebs 1999; C. J. Krebs and others unpublished) and, because hares were trapped on up to three control sites, variation existed in the mean density among sites (Hodges and others 2001). We used the latter estimate of mean (SD) hare density because we were more interested in

Table 3. Parameter Values for Monte Carlo Simulations of Snowshoe Hare Ecotrophic Efficiency from O'Donoghue (1994) and Stefan (1998)

	Peak 1988–89	Decline 1990–91	Low 1992–93	Increase 1994–95
Fall density (ha^{-1})	2.28 (0) [1]	1.62 (0) [1]	0.13 (0.005) [3]	0.53 (0.15) [3]
Spring density (ha^{-1})	0.74 (0.54) [3]	0.87 (0.09) [2]	0.08 (0.02) [3]	0.18 (0.10) [3]
Adult individual biomass (kg)	1.51 (0.17) [70]	1.46 (0.14) [83]	1.33 (0.15) [11]	1.41 (0.10) [25]
Proportion female	0.42 [72]	0.39 [87]	0.50 [12]	0.37 [28]
Proportion reproductive				
Litter 1	0.94 [32]	1.0 [7]	0.89 [23][a]	1.0 [17]
Litter 2	0.97 [31]	0.85 [13]	1.0 [17][a]	1.0 [17]
Litter 3	0.82 [34]	0 [13]	0.5 [8][a]	1.0 [12]
Litter size				
Litter 1	3.6 (0.9) [8]	3.3 (1.1) [7]	3.2 (1.0) [17][a]	3.0 (1.2) [6]
Litter 2	6.0 (1.4) [13]	4.2 (2.0) [11]	5.2 (2.1) [12][a]	6.9 (1.5) [9]
Litter 3	4.4 (1.1) [7]	—	3.2 (0.5) [11][a]	5.6 (1.7) [8]
Birth weight (g)				
Litter 1	52.7 (7.1) [7]	46.2 (4.5) [7]	51.8 (9.2) [13][a]	59.9 (8.8) [6]
Litter 2	54.3 (11.4) [12]	53.2 (10.3) [11]	54.8 (4.8) [10][a]	57.9 (7.5) [9]
Litter 3	69.3 (12.2) [7]	—	64.5 (4.7) [10][a]	70.3 (4.8) [7]
Leveret 30-d survival, transformed[b]				
Litter 1	1.02 (0.52) [12]	0.76 (0.49) [17]	0.52 (0.68) [36][a]	1.0 (0.52) [19]
Litter 2	0.49 (0.58) [23]	0 (0) [21]	0.45 (0.35) [50][a]	0.90 (0.49) [49]
Litter 3	0.44 (0.53) [11]	—	0.61 (0.27) [50][a]	0.89 (0.50) [31]

Values for numbers and biomasses are means (SD) [sample size]. Proportions are assumed to be binomially distributed; mean values [and sample sizes] are given.
[a]*All values are interpolated from data collected in spring 1992 and 1994 because reproductive data were not recorded in 1993.*
[b]*Leveret survival was available as Kaplan-Meier estimates (mean and SE). Prior to simulations, these values were arcsine-square root–transformed to improve normality. Transforming the SEs generated asymmetric variation around the transformed mean, but we assumed the variation to be normal and of intermediate magnitude. Random values were chosen from this new distribution, back-transformed to survival, and finally ln-transformed to provide daily mortality rates for use in Eqs. (1) and (6).*

the natural variation in hare densities that occurs in the boreal forest than in the variation accruing from methodological problems. Furthermore, the variation among grids was larger than the variation within grids.

Second, no data for hare reproduction were collected during the low phase in 1993. To model hare reproduction during the cyclic low phase, we averaged values from 1992 and 1994 and used the maximum standard deviation (SD). Survival of radio-tagged leverets was measured as 0 in 1992, but we know this value to be an underestimate of reproduction because some juvenile hares were captured in fall 1992. We parameterized the low-phase model by using both the mean and SD for leveret survival in 1994 divided by two, which probably yields an underestimate of true leveret survival in 1993.

Third, uncertainty in some parameters was sufficiently large that the probability density function encompassed unreasonable values. For instance, some randomly chosen values of peak hare densities were less than the average low density, and some survival values were less than 0% or more than 100%. When randomly chosen values for the simulations fell outside the realm of possibility, we chose new values. This strategy effectively reduced variation in parameter values and also led to directional change in the mean values of some parameters. For instance, during the peak, leveret survival was less than 0 for 20% of randomly chosen values for litters 2 and 3 and had to be reselected. Nevertheless, through these Monte Carlo simulations, we determined whether EE of hares at different stages of the cycle could be differentiated once uncertainty was incorporated.

Results

Insight into food web dynamics emerges from comparisons of EE and GE as the models become more realistic and in reference to different cyclic phases. All models of the Kluane boreal forest food web were based on the same trophic structure (Figure 1), yet they yielded different estimates of energy flow and conversion efficiencies (Figures 2–5). For all parameterizations, energy flow varied through the cycle. For the six herbivore taxa, EE varied by more than 50% through the cycle (Figure 2). EEs of carnivores varied only when we modeled annual changes in biomass,

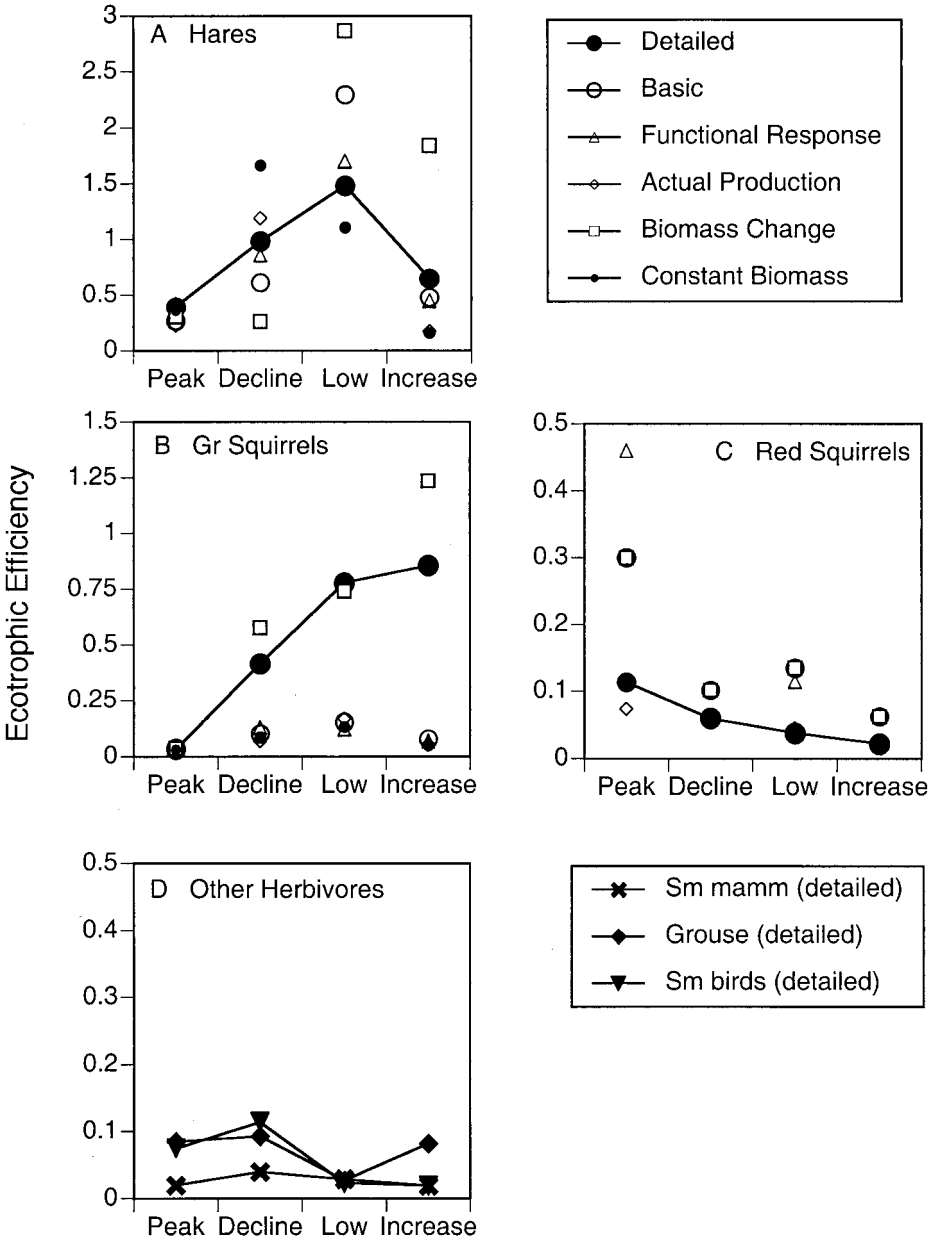


Figure 2. Ecotrophic efficiency (EE) throughout the cycle for (**A**) snowshoe hares, (**B**) ground squirrels, (**C**) red squirrels, and (**D**) other herbivores. Graphs (**A–C**) depict EE calculated from six different parameterizations of Ecopath. For other herbivores, EE was affected only by feeding rates of mammalian predators (allometric or functional response) and varied by up to 55% among parameterizations. Note the different y-axis scales.

because no other fates of production (for example, intraguild predation or trapping) were included. EEs varied 100% through the cycle for lynx, coyotes, great-horned owls and goshawks in the detailed and biomass change models, exceeding 0 during population increases.

The parts of the food web showing most variation in EE and GE do so for the following two reasons: (a) because production varies (as *P/B* increases, EE declines and GE increases), and (b) because consumption varies (as consumption increases, the GE of that taxon declines and the EEs of lower trophic levels increase). Most variation in energy flow is therefore due to within-species variation in net production and consumption; but in some cases, particularly for herbivores, EE varies due to consumption rates of predators (a between-species effect). Table 4 shows the range of variation in net production and consumption among species across the four phases and hence illustrates the diversity of values feeding into the Ecopath models for each phase. For five taxa (small mammals, grouse, small birds, Harlan's hawks, northern harriers), we lacked sufficient data to evaluate cyclic variation fully, so we devote little consideration to the among-phase results for these taxa.

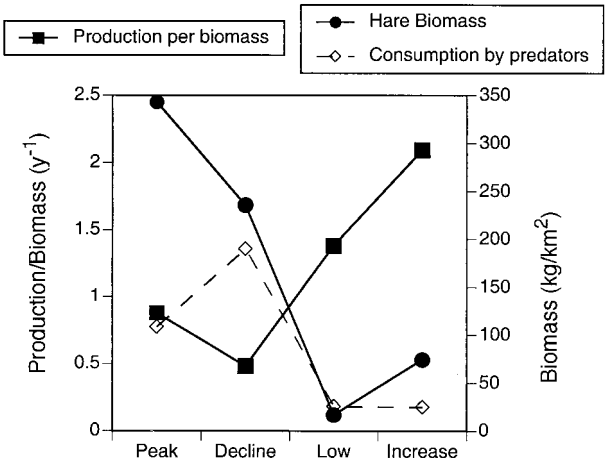


Figure 3. Components of hare ecotrophic efficiency (EE) in constant biomass parameterizations. Total production is the product of biomass and production per biomass (*P/B*). Consumption of hares combines effects of all predators and is a function of predator biomasses, feeding rates, and diet compositions.

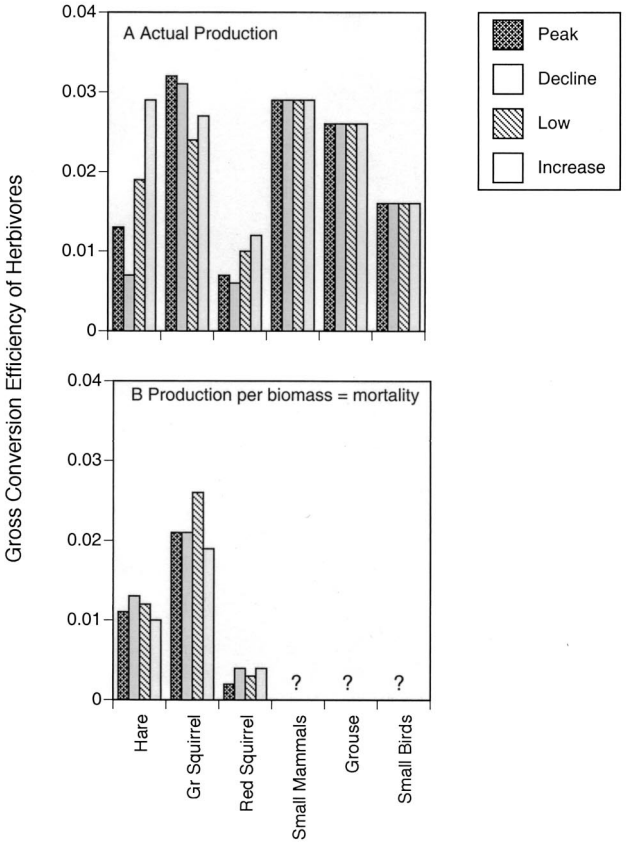


Figure 4. Gross conversion efficiency (GE) of herbivorous taxa under different model parameterizations. Conversion efficiency is dependent on production per biomass (*P/B*), which was modeled in two ways: (**A**) actual production, measured from reproduction and growth (detailed, actual production, constant biomass models), and (**B**) adult mortality rates (basic, biomass change, and functional response models).

Ecotrophic Efficiency

Ecotrophic efficiencies were less than 1 in all models for all herbivores except hares and ground squirrels (Figure 2). When EE is greater than 1, models are unbalanced because there is not enough production to account for all the fates of a species' biomass. Hares had EE greater than 1 in three general cases—for the actual production and constant biomass models of the decline (actual production was less than mortality and the biomass decline was not incorporated); for the biomass change model of the increase (*P/B* was low because mortality was low but biomass increase was incorporated); and for all models during the cyclic low. Ground squirrels had an EE greater than 1 only for the increase biomass change model, suggesting that *P/B* equal to mortality could not account for observed population increases. For small mammals, grouse, and small birds, EEs were low but variable; this variation was due to parameterizations of predators, because their own production was assumed to be constant through the cycle and across model types.

Snowshoe Hares. The detailed and constant biomass models produced EE approximately equal to 1 for snowshoe hares during the decline and low, just as would be expected if predators consume standing stock in addition to production (Figure 2A). In contrast, snowshoe hare declines would not have been expected based on basic models (EE equals 0.55), and both basic and biomass change models were highly unbalanced (EE greater than 1) during the low. Changing the models to incorporate actual production or predator functional responses brought the models closer to observed dynamics, essentially raising consumption relative to production of hares during the decline, and lowering that ratio during the low phase. Increases in hare densities were only likely when *P/B* equals actual production rather than adult mortality (detailed versus biomass change models during the increase phase). The large distinction in model results related to using actual production versus adult mortality for *P/B* of hares occurred because mortality and reproduction tended to be inversely correlated.

The results from constant biomass models highlight the consumption of a species relative to its production and therefore indicate trophic links for which top–down impacts are likely to occur. Snowshoe hares had their lowest EEs—0.16 and 0.36—

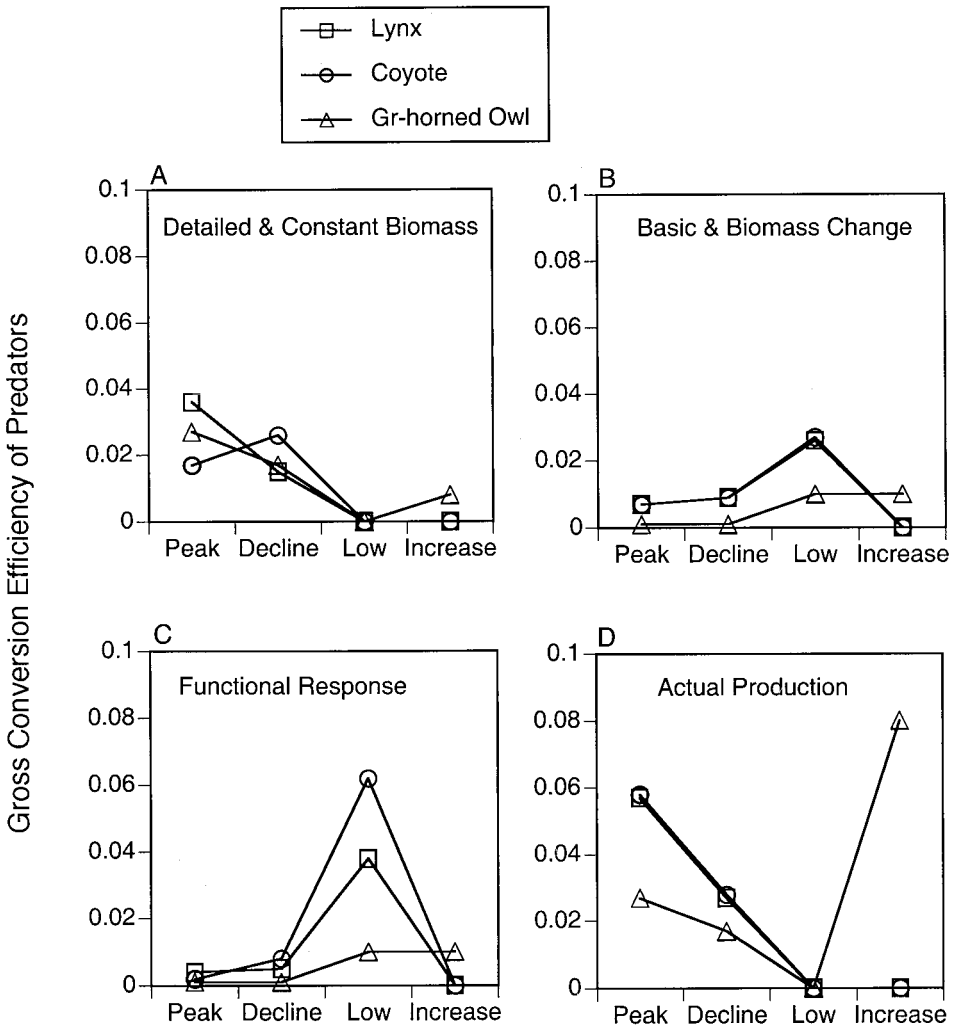


Figure 5. Gross conversion efficiency (GE) of predator taxa calculated from six different parameterizations of Ecopath. Conversion efficiency is dependent on production per biomass (*P/B*), which was modeled from reproduction and growth data or as equivalent to adult mortality, and consumption per biomass (*Q/B*), which was modeled from field data or allometrically. Basic and biomass change models yield the same results because both are based on *P/B* equal to mortality and allometric *Q/B*; similarly, detailed and constant biomass models yield the same results because both are based on *P/B* equal to actual production and *Q/B* equal to observed feeding rate of mammalian predators. (**A**) Detailed and constant biomass models, (**B**) basic and biomass change models, (**C**) functional response model, (**D**) actual production model.

during the increase and peak phases, respectively, and had much higher EEs—1.67 and 1.10—during the decline and low phases (Figure 2A). The 10-fold difference in hare EEs, and EE greater than 1 in two cyclic phases, indicate a dramatic variation in the strength of the top–down effect of predators on hares. During periods of biomass decline, all of the snowshoe hare production and some of the standing stock were consumed by predators. As hares increased, predators still consumed more of the production than they did for the other herbivorous taxa, but hare production exceeded predator consumption.

Because of the central role of hares in the boreal forest food web (Ruesink and Hodges 2001), we explored EE in more depth by examining the cyclic changes in parameters contributing to EE. In Figure 3, we present the parameters that compose EE—standing biomass of hares, production per biomass, and biomass of hares consumed. These factors show whether shifts in population trajectories can be attributed to how many hares are present, their per capita reproductive rates, or predation pressure. In the decline phase, two factors changed relative to the previous phase—predator numbers increased (as indicated by consumption of hares) and hare *P/B* declined. The decline phase of the cycle appears to be caused by a combination of top–down and bottom–up changes, with high consumption of hares not compensated for by low per capita reproduction. Similarly, both production and predation interact to allow the shift from low to increasing hare densities. The low and increase phases were equivalent in terms of consumption of hares, but hares had slightly higher biomass and per capita production during the shift from low phase to increase, which was sufficient for them to "escape" control by predators.

Other Herbivores. Relative to hares, other herbivores had lower EEs in constant biomass models,

Table 4. Summary of How Parameters Varied among Phases of the Cycle, Showing Range of Field Measurements for 4 Modeled Years of Detailed Models

	Biomass (kg/km^2)	Production/Biomass (P/B) (y^{-1})	Consumption/Biomass (Q/B) (y^{-1})	Annual Biomass Change (ΔB) (kg/km^2)
Snowshoe hares	17–343	0.48–2.10	71	−78–+76
Ground squirrels	45–107	0.78–1.02	32[a]	+22–+56[b]
Red squirrels	61	0.72–1.43	115	0
Lynx	0.24–1.77	0–2.06	25–67	–0.94–+1.00
Coyotes	0.20–0.99	0–2.06[c]	15–123	–0.42–+0.26
Great-horned owl	0.31–1.16	0–1.05	39	–0.48–+0.17
Goshawk	0.02–0.06	0.5–1.5	42	–0.02–+0.06
Harlan's hawk	0.22	0.3–0.8	14[a]	0
Northern harrier	0.04	0.9–2.0	17[a]	0

Demographic measurements for grouse, small mammals, and small birds also varied among years, but this variation was not incorporated because its magnitude was small or uncertain. In most cases, parameters modeled with cyclic variation were also modeled differently among parameterization methods. Exceptions, which were consistent among all parameterizations, were starting biomasses of all taxa and P/B values of goshawks, Harlan's hawks, and northern harriers. Diet composition varied through the cycle for all predators but was kept constant among different parameterization methods.
[a]*Q/B reduced to one-third for migratory and hibernating species (also includes small birds).*
[b]*Ground squirrel changes in biomass were modeled only after 1991.*
[c]*Coyote P/B values were assumed to equal lynx values.*

indicating that they were less likely to be predator-limited. Of course, several predators not included in these models (mustelids, foxes, other raptors) would undoubtedly raise EEs of these alternative prey. Even in this restricted food web, however, there was substantial variation in EE for herbivores other than hares. For red squirrels, grouse, and small birds, EEs were highest when predators were abundant during the peak and decline phases. For ground squirrels, however, EE was highest when predators were rare, probably due to a combination of relatively low ground squirrel biomass (therefore little production) and larger proportions of ground squirrels in the diets of predators (ground squirrels as a percentage of diet compositions rose by up to 20%) (Doyle and Smith 2001).

For red squirrels and ground squirrels, basic models yielded low EEs through the cyclic phases, with EEs ranging from 0.06 to 0.30 and 0.04 to 0.15 for the two species (Figures 2B and C). Ground squirrels have generally been shown to undergo population cycles in concert with hares (Boutin and others 1995), but in the years we modeled, ground squirrels consistently increased (Boonstra and others 2001a). Thus, incorporating biomass change led to much higher EEs of 0.58, 0.74, and 1.24 during the decline, low, and increase phases, respectively; but detailed models all had EE less than 1, meaning that these increases were possible given actual production and predation (Figure 2B). For both squirrel species, P/B was generally higher when calculated from actual production than from adult mortality; consequently, EEs in actual production models were lower than in basic models. Because red squirrels were given constant biomass in all models, basic and biomass change EEs were identical, as were detailed and constant biomass EEs (Figure 2C). Modeling the functional response of predators led to a greatly increased EE for red squirrels during the peak phase (from 0.30 to 0.46), but caused little change during the other phases. Modeling the functional response had a proportionally smaller effect on the EEs of ground squirrels (from 0.037 to 0.047) because feeding rate changes in mammalian predators were diluted by constant (allometric) feeding by avian predators

Predators. The EEs for predators were always 0 unless biomass change was incorporated (biomass change and detailed models), because we included no fates for predator production other than biomass accumulation. Harlan's hawks and northern harriers always had EE equal to 0 because their populations were assumed invariant. For other predators, EE was greater than 0 in models and years when biomass increased. In detailed models, production kept pace with biomass increases for lynx, coyotes, and great-horned owls during the peak phase, but did not match empirical population increases of goshawks at the peak and low. Furthermore, lynx and coyotes increased in density in 1994–95 (hare increase phase) when no predator reproduction was observed (O'Donoghue and others 1997); their EEs for detailed and biomass change models were effectively infinite. The biomass change models

generated EE greater than 1 for all four cyclic predators during the peak. These high EEs occurred because production was modeled after adult mortality—which was lower than actual production—while the biomass increased.

Gross Conversion Efficiency of Herbivores

Only two patterns for herbivore GE emerged from the six methods of parameterizing Ecopath models (Figure 4). This result occurred because the consumption component of GE was always based on allometry, while the production component for snowshoe hares, red squirrels, and ground squirrels took on one of two parameterizations—actual production (actual production, constant biomass, and detailed models) or adult mortality (basic, biomass change, and functional response models). Variable GEs (0.007–0.029) based on actual production by hares reflect substantial variation in reproduction through the cycle (because consumption was assumed constant). For red squirrels and ground squirrels, reproductive output was much more consistent over time, thus resulting in fairly steady GEs (0.006–0.012 and 0.024–0.032, respectively). Using the second parameterization method, of *P/B* equal to mortality, GEs were lowered for snowshoe hares, ground squirrels, and red squirrels. Additionally, hare GEs were much more consistent with this parameterization, ranging only between 0.010 and 0.013. There were only single estimates of *P/B* for small mammals, grouse, and small birds, and these estimates were considered invariant across cyclic phases, so these three taxa had single values for GE of 0.029, 0.026, and 0.016, respectively. Small birds had particularly high GE because we incorporated just 3 months of summer feeding.

Gross Conversion Efficiency of Predators

For mammalian predators, we were able to parameterize both production and consumption from field estimates. We therefore generated four estimates of GE from the six models. Basic and biomass change models were the same with respect to GE, as were detailed and constant biomass models. The basic and biomass change models yielded the highest GEs during the low phase (0.026 for lynx, 0.027 for coyote) (Figure 5), reflecting high mortality (equal to *P/B*). In other phases, GEs were less than 0.009. This temporal pattern was mirrored in the functional response model, but because observed feeding rates were lower than allometric during the low phase, GEs were higher. The actual production model produced the inverse temporal pattern, with GEs of 0 during the low phase and GEs of 0.057 and 0.027 during the peak and decline phases. The detailed model produced relatively low GEs overall (less than 0.04), with the lowest GEs in the low and early increase phases when little predator reproduction occurred. GEs at other phases reflected kill rates rather than actual consumption, and lowering assimilation to account for surplus killing would tend to raise GEs during phases when mammalian predators reproduced.

For avian predators, we only had allometric estimates of consumption rates. *P/B* varied through the cycle for all species based on fledging success, but adult mortality data (and thus a second parameterization method) existed only for great-horned owls. Therefore, GE changed through the cycle with fledging success rates, which were generally highest when hares were abundant (goshawk GE equals 0.036 at the peak, Harlan's hawk GE equals 0.058 at the low, northern harrier GE equals 0.119 at the peak, great-horned owl GE equals 0.027 at the peak). Values were three times too high for migratory species (Harlan's hawk and northern harrier) because we included only summer consumption. As with mammalian predators, using *P/B* equal to adult mortality for owls reversed the cyclic pattern of GE, resulting in unlikely values of 0.01 when hares were rare and 0.001 when hares were common (Figure 5).

Modeling Uncertainty in Snowshoe Hare Production

The point estimates of EE calculated with Ecopath obscure substantial uncertainty in estimates of energy flow (Figure 6). Based on Monte Carlo simulations, the 95% confidence bands around EE of snowshoe hares were as large as median values. Nonetheless, these simulations indicate that Ecopath successfully described cyclic differences in energy flow: Both Ecopath and Monte Carlo simulations calculated that EE of hares differed systematically through the cycle (Increase $\approx$ Peak $<$ Low $<$ Decline). In all cases, the value of EE we obtained from mean parameter estimates fell within the 95% confidence limits (CL) of the simulated values. Monte Carlo simulations produced some bias in EE. At the peak and low, the EE generated by Ecopath was two times higher than the median value from simulations. However, population cycles still emerged. Specifically, during increase and peak phases, less than 10% of simulations produced EE greater than 1, so biomass could increase; whereas during the decline and low, more than 80% of simulations would require a loss of hare biomass in order to balance. Decline and low phase EEs calculated in Ecopath fell outside the

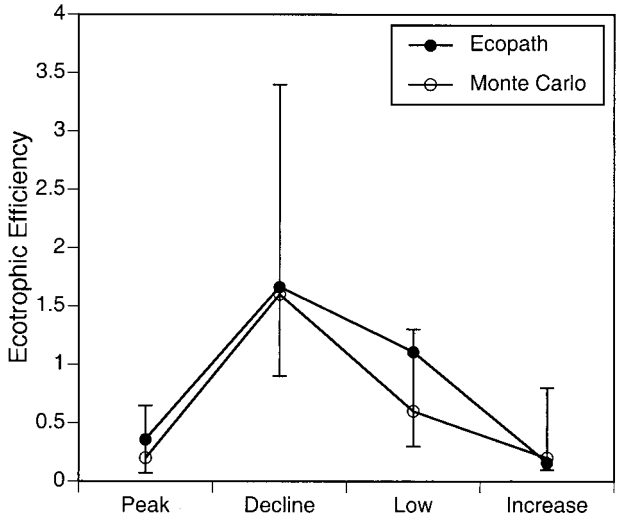


Figure 6. Uncertainty in ecotrophic efficiency (EE) of hares based on Monte Carlo simulations incorporating variance in parameter estimates. Monte Carlo results are presented as median ± 95% CL based on 200 simulation runs. For comparison, we show the single values of EE calculated via Ecopath for constant biomass models.

95% CL of simulations for the increase and peak, and vice versa. Therefore, these phases of the cycle are marked by significantly different pictures of top–down effects on snowshoe hares.

Discussion

The Ecopath models we generated show one clear modeling effect and two general biological patterns. Methodologically, the parameterization technique has large impacts on the estimates of ecotrophic and conversion efficiencies for many of the taxa. For example, cyclic patterns of GE were inverted between functional response and actual production models for predators (Figure 5). Biologically, differences in the strength of top–down effects exist among species and among phases of the hare cycle, as highlighted by the variable EEs of herbivores (Figure 2). Finally, because GE is a physiological parameter and expected to stay relatively constant, the observed differences in productivity through the cycle imply strong bottom–up effects on species such as hares, great-horned owls, and mammalian predators (Figures 4 and 5).

Insights from Different Parameterization Methods

Detailed models, which incorporated realistic data on production, consumption, and density fluctuations, outperformed the models containing one or all of the simplifying assumptions of *P/B* equals mortality, no functional responses, and no biomass change. The detailed models did better at matching conspicuous dynamics, such as fluctuations in biomass and reproduction when food was abundant. Interestingly, detailed models had essentially the same proportion of cases that violated thermodynamic principles (EE greater than 1 in five of 48 cases [10%] versus 26 of 240 cases [11%] for other models). However, detailed models often brought EEs closer to 1 when other parameterizations had values that were very low or very high, and they generated GEs that were most consistent through the cycle (Figures 2, 4, and 5). Comparing detailed models to other parameterizations generates explicit insight into the roles of production and consumption in the dynamics of this cyclic system. Of course, because we use data for a single cycle at a single location, we cannot determine how our conclusions apply to boreal forest food webs in general.

Constant biomass models highlighted the relative values of actual production and consumption rates, thus giving the clearest indication of how much production by a taxon is consumed. When EE was much greater 1 in constant biomass models (for example, hares during the decline phase), incorporating the observed drop in hare density eliminated the imbalance in EE (detailed model). Conversely, if a taxon does not increase in biomass when EE is much less than 1 in constant biomass models, then it must be limited by some factor other than predation from taxa in the model; small birds and small mammals provide good examples of this pattern (Figure 2). In this context, it should be noted that we did not model all of the mammalian or avian species at Kluane. For example, weasels (although relatively rare) are probably the main predator of small mammals, and including weasels in Ecopath models would clearly lead to higher EEs for voles and mice. The constant biomass models thus reveal the extent to which predators that rely on snowshoe hares affect other prey species in this food web, but these models do not exhaustively characterize the dynamics of all vertebrate taxa at Kluane.

It is not at all surprising that parameterizing *P/B* as adult mortality would fail in this nonequilibrial food web. An excess of production over mortality is required for biomass to accumulate, so of necessity mortality was lower than actual production for cases such as lynx at peak hare densities and hares during the increase phase. Similarly, mortality must exceed production for standing biomass to decline. Defining *P/B* as equal to mortality therefore leads to cycles of the wrong shape. During periods of population decline, production is overestimated be-

cause mortality is high, thus predicting slower declines; whereas during population increases production is underestimated, predicting slower growth.

Parameterizing *P/B* as adult mortality is least effective when survival and reproduction are positively correlated through the cycle. Precisely when actual production is high, mortality rates generate a low estimate of *P/B*. This appears to be the case for hares and several predators but not for red squirrels. During the four phases modeled, actual production of red squirrels was calculated as 1.7–4.2 times higher than adult mortality. For ground squirrels, actual production was never more than 0.5 times higher than adult mortality; while during the low phase, adult mortality exceeded production. Despite estimates of production that were similar to estimates of mortality, biomass increased in all of our modeled years except 1988–89, for which we had no data. This imbalance indicates that either survival or production was underestimated for ground squirrels.

Independent adult mortality estimates for other herbivores at Kluane do not exist or are based on small sample sizes; they are likely to be similar in demography to red squirrels, with survival and reproduction not correlated. It has been suggested that cyclic species such as hares and ground squirrels should have relatively elastic annual reproductive output to achieve dramatic population increases under favorable environmental conditions (Cary and Keith 1979; O'Donoghue and Krebs 1992; Stefan 1998; Karels and others 2000). In contrast, our calculations show that red squirrels are more variable in actual production than are ground squirrels (Table 4); red squirrels may fail to cycle because adults are long lived (Table 2) and difficult to catch (Oksanen 1992), thus buffering the population against declines. Red squirrels also experience an unpredictable environment with respect to food supply. Conditions are most favorable for reproduction during mast years for spruce cones (Boonstra and others 2001a, 2001b).

Using mortality as a surrogate for *P/B* in these models also undermines gross conversion efficiency (GE). For predators during the low phase, survival was low, so this metric of *P/B* was high in the basic and biomass change models. In the functional response models, the problem was exacerbated for mammalian predators because their feeding rates were low when mortality was high. Accordingly, functional response models resulted in impossibly high GEs during the low (6% conversion), or an order of magnitude more production per food intake than was indicated during other phases of the cycle, but at a time when reproduction was actually limited to nonexistent (Figure 5).

Functional responses of predators contributed to the cyclic dynamics of the boreal forest food web. Lynx and coyotes conducted more surplus killing of hares and ate less of each carcass when hares were abundant than when they were scarce (O'Donoghue and others 1998a). Consequently, modeling functional responses tended to raise hare EE at the peak and reduce it at the low. Most importantly, if predators fed at a constant rate through the cycle, the decline in hare abundances would not be as large as observed. Our models were based solely on the functional responses of lynx and coyotes because we lacked data on the functional responses of raptors. If raptors also exhibit functional responses, the effect on hares and hare EEs would be even more pronounced.

Data and Assumptions: The Issue of Error

Different parameterization methods clearly generate different patterns of EE among taxa and phases of the cycle (Figure 2). In addition, regardless of how parameter values are calculated, each parameter also has an associated error, within which equivalent dynamics might not be predicted. In Monte Carlo simulations incorporating uncertainty in demographic parameters of snowshoe hares, calculated EEs had wide confidence limits (median less than 95% CL) (Figure 6). However, uncertainty did not alter our conclusions about snowshoe hare dynamics, which is reassuring given that hares are a central component of the boreal forest food web. Variation in hare EE increased with variation in parameters, but cycles remained. Specifically, EE was large during the decline and low phases when hares were predator-limited, and EE was lowest during the population increase (Figure 6). These patterns suggest that for the Kluane system, obtaining meaningful model results was more affected by parameterization method than by error in estimating parameter values.

Despite this conclusion, and despite the decades of careful study that have addressed the boreal forest food web, data with less uncertainty would still help us to understand population and community dynamics in detail. Many parameter values were based on low sample sizes and have wide confidence intervals. Inaccurate mean values could account for the thermodynamic impossibilities that remained even in detailed models (Figure 2). Indeed, the confidence limits calculated for EEs of hares in the Monte Carlo simulations were wide enough to "fix" most cases of EE greater than 1 in the detailed models. In short, given uncertainty in parameter values, all detailed models should balance, except when predators increased in

density but were not observed to reproduce (implying immigration). In contrast, other analyses of the hare cycle that incorporate uncertainty in parameter values have not been able to balance production and mortality. In a stage-structured stochastic demographic model using Kluane data from 1995–96, Haydon and others (1999) found that the estimates of snowshoe hare fecundity and survival rates were too low to account for the observed population increase. They speculated that survival rates may be underestimated by current methods, perhaps because handling animals increases the chance that they or their offspring will die.

Nonequilibrial Food Webs and Changing Predator–Prey Interactions

The nonequilibrial nature of the boreal food web cannot be summarized by a single mass-balance model but instead would be best encapsulated by separate models for each year of the approximately 10-year hare cycle. Based on flows of biomass (EE and GE) in the detailed models of the four cyclic phases, there is cyclic variation in the strength of top–down and bottom–up interactions in the food web. Snowshoe hares showed the greatest variation in EE among herbivores: Both production and predation rates fluctuated dramatically, combining to influence hare EE. In particular, the decline phase was associated with high mortality due to predation (predator densities and kill rates were high) and low per capita reproduction (Figure 3). The cause of this reduced reproductive rate remains unknown, but it could include a lack of high-quality food, reduced foraging to avoid predation, or physiological stress induced by high predator densities (Cary and Keith 1979; Vaughan and Keith 1981; Hik 1995; Boonstra and others 1998).

It has been argued that the transition from peak densities to declining densities occurs because of an interaction between top–down and bottom–up factors: Hare production drops and is exceeded by mortality induced by predators (Krebs and others 1995). In our detailed model, *P/B* was relatively low at the peak and consumption of hares was high; however, EE remained less than 1 (0.40), which indicates the possibility of continued biomass increase by hares. During peak densities, hares were so abundant that even low per capita production resulted in high total production. Therefore, reduced reproduction by itself was not nearly enough to initiate the decline; high mortality rates were also necessary. But for predators to cause this plateau requires numerical and functional responses—perhaps even additional predator species—not currently incorporated in the models. It is possible that predation by some of the other boreal carnivores, such as wolverine (*Gulo gulo*), marten (*Martes pennanti*), wolves (*Canis lupus*), and hawk owls (*Surnia ulula*) that display functional responses to hares would be sufficient to cause consumption to exceed production of hares (Theberge and Wedeles 1989; Dibello and others 1990; McIntyre and Adams 1999). Keith (1981, 1990) has suggested that overwinter food shortage causes the decline by leading to reduced reproduction and high starvation rates. Empirical work and food addition experiments have failed to support the contention that starvation is able to initiate the decline because the mortality needed is simply too high (Krebs and others 1986a, 1986b, 1995; Hodges and others 2001). These results strongly indicate that predation is a necessary cause of the cyclic decline.

Due to interactions with predators, which showed striking variation in biomass and functional responses, herbivores other than hares also varied cyclically in EE. Theoretically, predators could have the greatest impact on other herbivores during the low phase if they switched from hunting hares to hunting other prey species (Sinclair and others 1998). Alternatively, predators could have the greatest impact on other herbivores when predator abundance is high during the peak and early decline phases of the hare cycle, even if predators predominantly eat hares (Pech and others 1995; Sinclair and others 1998). Both experimental evidence and the Ecopath results suggest the latter scenario because high predator densities resulted in a higher predation rate on other herbivorous species despite the functional response of predators to hares (Figure 2) (Stuart-Smith and Boutin 1995; Martin and others 2001).

Ground squirrels present something of a special case. Although their EEs were lower than those of hares, they were higher than those of other herbivores in this system. Experimental evidence suggests that they are partially regulated by predation (Karels and others 2000). Because ground squirrels hibernate, up to 50% of their biomass is unavailable to predators because mortality occurs overwinter in hibernacula (Karels and others 2000). Modeling only the available ground squirrel biomass would therefore double EE, supporting the idea that ground squirrels are influenced by top–down interactions. Ground squirrel EE was highest when hares and predators were least abundant. During this time, predators altered their diet composition to include more ground squirrels (average across six predator taxa equals 15% at peak and 25% at low). Ground squirrels thus showed the inverse pattern to the other herbivores because their own biomass

was low during the low of the hare cycle, and ground squirrels provided the major alternative prey item for many of the predators (Doyle and Smith 1994, 2001).

Bottom–up effects in this food web were evident primarily in GEs of cyclic predators. Successful reproduction by predators such as lynx, coyotes, and great-horned owls did not occur until the food supply exceeded threshold levels (see also Slough and Mowat 1996; Stenseth and others 1997; Mowat and others 2000). Snowshoe hares also showed striking differences in GE through the cycle, from 0.007 to 0.029 in detailed models. If this plastic GE is accurate, it indicates a lack of bottom–up effects for hares: similar feeding led to different production through the cycle, so population dynamics shifts are not easily attributed to food supply. Alternatively, feeding by hares may be more variable than allometry would suggest. Furthermore, changes in plant nutritional and defensive chemistry through the cycle may lead to changes in hare reproduction even if actual biomass intake remains constant, although this linkage has yet to be substantiated (Bryant 1981; Sinclair and others 1988; Keith 1990). In any case, our findings do not support the common proposition that GE is a species-specific constant (Peters 1983).

Conclusions

The main conclusion of our analysis is that top–down impacts predominate in the snowshoe hare–dominated boreal forest ecosystem. The resulting system is not, however, similar to the trophic cascades described for aquatic ecosystems (Strong 1992; Pace and others 1999) because the boreal food web is largely cyclic or nonequilibrial in the short term. Herbivores exert strong impacts on plants in this ecosystem, but these are temporary impacts and are reduced once predators become abundant (Krebs and others 2001b).

Because parameter values for densities and demographics are so unusually well known for this boreal forest food web, we did not attempt to "balance" the models by altering values until all EEs approximated 1. Instead, the imbalances and differences among species and phases of the cycle were the sources of greatest insight into these nonequilibrial dynamics. The Ecopath results reinforce an emerging picture that the snowshoe hare cycle occurs due to a combination of shifts in production and depredation of hares, with predation essential to the decline and low phase, and increasing reproduction essential for the shift from low to increasing hare densities (Krebs and others 1995, 1998; Krebs 1996; Stenseth and others 1997). Species that interact directly with hares (predators) can respond dramatically to changes in population density of hares. Other herbivores, which interact indirectly with hares via shared predators, are weakly if at all cyclic, although EEs do vary. After hares, ground squirrels show the next highest herbivore EEs and the next most variable EEs; they act as an important alternative prey of food-stressed predators during the hare low phase. The other herbivores have their highest EEs during periods of elevated hare abundance, suggesting an impact of incidental predation by abundant hare predators; this pattern is confirmed by analyses of predation patterns (Stuart-Smith and Boutin 1995; Martin and others 2001).

This food web is characterized by shifts in the strength of top–down and bottom–up interactions among the vertebrate taxa. Although we did not model plants and their consumption, we expect that a similar pattern occurs. Further understanding of the cycle is likely to come about by determining the causes of shifts in hare reproduction and by exploring the conditions that generate cycles of different duration and amplitude. For example, it is possible that high-amplitude peaks of hares occur when there are exceptionally good growing conditions for plants because of bottom–up effects on hare reproduction, or when predator populations are depressed by human hunting and trapping, resulting in lower predation rates. Our results suggest that other predators in the boreal forest may contribute to hare cyclicity even if they do not show numerical responses to the cycle. Ultimately, further exploration of the functional and numerical responses of the entire predator guild along with estimates of intraguild predation rates will prove useful.

Uncertainty in parameter values appears not to influence the overall picture of biomass flow unduly, but the method of parameterization employed is extremely important. Common assumptions about production, consumption, and biomass stability result in patterns of EE and GE that do not match the empirically observed dynamics of this fluctuating system. Given sensible parameterization methods, however, the Ecopath approach shows promise for exploring ecosystem dynamics even under nonequilibrial conditions. Population ecology has progressed during the last 50 years largely because it has a rigorous population arithmetic available to see if the books balance. Community ecology has largely lacked this type of ecological arithmetic, with the exception of nutrient cycling and stoichiometry, making it difficult to determine whether the flows of materials and energy balance.

Using Ecopath, we have combined detailed organismal data with the grand picture of energy flow in a way that reveals whether demographic understanding yields balanced community dynamics.

There remains the question of whether we could have developed a detailed understanding of the boreal forest community by the use of Ecopath without field experimentation. Ecopath can provide valuable insights as a detailed description of ecosystem interactions, but we remain convinced that experimental manipulations are still desirable to test the conjectures that flow from Ecopath. In fact, it is now possible to construct "what if" scenarios in the modeling framework (such as what happens when terrestrial predators are removed, or what happens in the absence of ground squirrels) that could subsequently be tested with experiments. However, Ecopath might fall short in ecological prediction because of unexpectedly strong indirect effects occurring among species, or behaviors such as predator avoidance that vary with predator density.

A real advantage of the Ecopath approach is that it quantifies the strength of species interactions without the requirement of direct measurement (compare Paine 1992). In the cyclic system at Kluane, temporal variation in the strength of trophic interactions among "driver" species was a hallmark of nonequilibrial dynamics (Ruesink and Hodges 2001). Along with Walters and others (1997), and as indicated by the sensitivity of our results to the method of parameterization, we conclude that complex multispecies systems contain a particular subset of all possible interactions that results in overall persistence despite perturbations and fluctuations. That persistence can emerge from nonequilibrial dynamics is an important principle in understanding how ecosystems function.

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