19

Trophic Mass Flow Models of the Kluane Boreal Forest Ecosystem

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The Kluane ecosystem project has generated detailed demographic portraits for many species that inhabit the boreal forest. The experimental manipulations have allowed us to test the impacts of food and predation on the population densities and demography of a number of herbivorous species, as well as to compare the strength of bottom-up versus top-down interactions among trophic levels (chapter 17). At Kluane we documented cycles occurring not only in species' abundances, but also in survival, reproduction, and diet composition. A striking general result from the Kluane studies is the huge shift in biomass in the forest throughout the 10-year cycle. Not only does overall herbivore biomass change more than threefold, but also the amount of the herbivore biomass represented by snowshoe hares varies from about 65% at the peak down to about 10% during the low phase (figure 19.1; CD-ROM frame 70). Predator biomass shows a similar overall shift, although no individual predator fluctuates as much in its proportional representation (figure 19.2). The dynamics of this multispecies food web may change substantially over the snowshoe hare cycle as a result of these biomass shifts.

In this chapter, we present a series of food web models to explore the impacts of these changes in biomass on the trophic interactions within the Kluane ecosystem. Specifically, we examine how the connections in this food web, as indicated by biomass flows, change through the cycle, between seasons, and when portions of the food web are manipulated experimentally. We concentrate on the interactions among vertebrates rather than exploring plant–herbivore interactions in any depth, largely because changes in plant biomass are less dramatic than the vertebrate responses due to the large reservoir of biomass in the woody material of trees and shrubs. We therefore restrict our examination of plant–herbivore interactions to analyzing the estimated total biomass of plant material necessary for the offtake by herbivores. For herbivore–predator interactions, we examine biomass flow on a per species basis. The two model outputs of total offtake of plant biomass and species-specific mass balance (i.e., the amount of a species consumed relative to its production) allow us to identify both strong interactions and portions of the food web in need of further study.

The Kluane ecosystem was chosen for an ecosystem study partially for its tractability, in that there are only a handful of species at each trophic level compared with the species diversity in other forested ecosystems. But even with detailed demographic information for many of the Kluane vertebrates, the ecosystem dynamics are not immediately obvious. The approximately 60-fold difference in individual body mass among herbivores (i.e., hares of ~1500 g and microtines of ~25 g) means that even identical demography or abundances of these two groups would have very different implications for their forage plants and their predators. This is because the species eat different plants at different rates, and predators differentially prey on species of varying sizes. Exploring trophic interactions using total biomass instead of abundance does not overcome problems of body size because metabolic rate scales nonlinearly with body size across species (Peters 1983).

To solve these problems, taxonomic uniqueness must be maintained while using a framework with a single and comparable currency. In our food web models, we convert every demographic change into a change in biomass for that species, and predator–prey interactions are similarly modeled as intake of biomass of each herbivore species per unit of predator biomass. In this fashion, demographic changes are all brought into a single

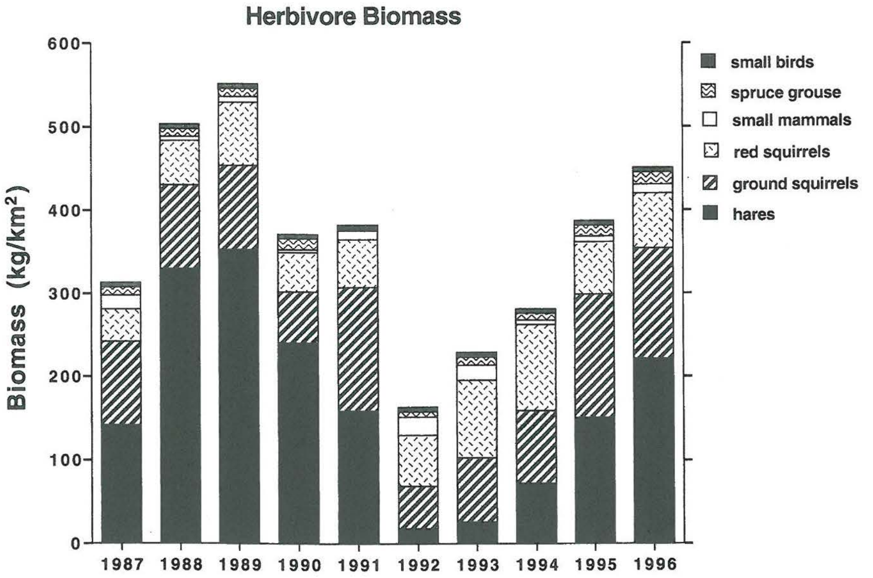

Figure 19.1 Biomass of herbivores in the boreal forest. Snowshoe hares accounted for 11–66% of total herbivore biomass, and ground squirrels 17–39%.

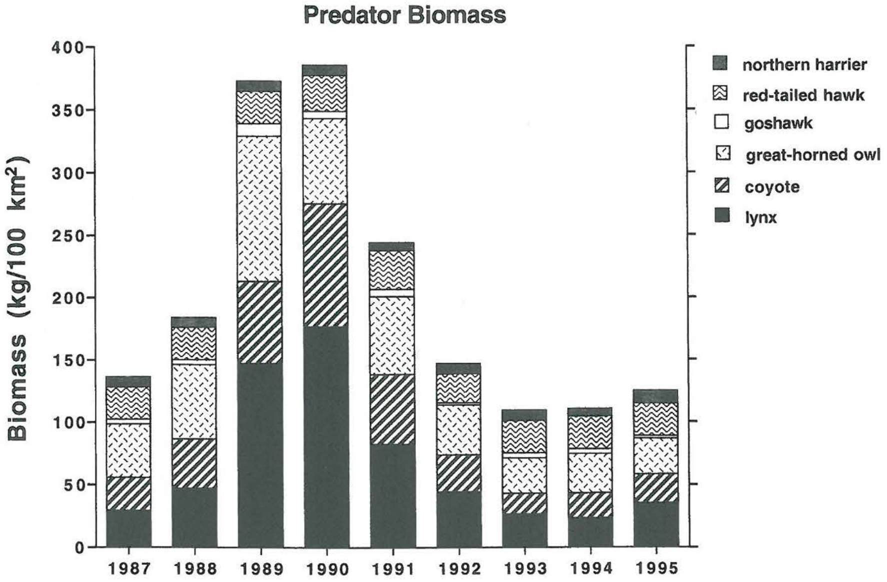

Figure 19.2 Biomass of predators in the boreal forest. Proportional biomass of lynx ranged from 21% to 46%, coyotes 15% to 26%, and great horned owls 18% to 32%.

currency that automatically weights the relative contribution of a species or of a demographic change to the biomass in the entire ecosystem.

19.1 Questions about the Ecosystem Dynamics of the Boreal Forest

As the previous chapters in this book have illustrated, most species at Kluane have extremely variable reproduction and survival, whether related to the hare cycle (e.g., coyotes, lynx, great horned owls, spruce grouse, ground squirrels) or independent of the hare cycle (e.g., red squirrels, microtine rodents). Some species also vary through the cycle in feeding rate and diet composition. This complexity in the ecosystem would allow an infinite series of explorative models. We focused on five main questions that address the large ecosystem questions related to the snowshoe hare cycle and the experimental manipulations.

1. How do trophic interactions change through the four phases of the cycle?
2. What are the impacts of food addition on the trophic interactions?
3. What are the impacts of predator reduction on the trophic interactions?
4. What are the effects of running models from spring to spring versus autumn to autumn?
5. How do the model outputs change when the models exclude one dominant species (snowshoe hares) or many that are rare, small, or noncyclic (most herbivores and raptors)?

The rationale for exploring the cyclic phases is obvious: fluctuations in biomass, relative biomass, and demography could alter the extent to which biomass offtake is balanced by production. We examine the impacts of food addition and predator removal because of the impacts these manipulations had on the demography of several herbivorous species, most notably snowshoe hares and ground squirrels (chapters 8, 9). Food addition primarily affected herbivore production, and its influence should vary by phase of the cycle because the hare peak and low correspond to times when food should be most and least limiting, respectively. Predator exclosure primarily affected depredation of herbivores, and its influence also should vary with cyclic phase, with predation least and most severe during the increase and decline phases, respectively.

We explore seasonality because of the risk that different initial conditions could affect model outputs. Most production (reproduction and growth) occurs in summer, whereas most consumption occurs in winter because winter spans 8 months of the year. Thus, for the species for which we have data from two annual censuses, autumn biomass exceeds spring biomass. The yearly change in biomass also varies by season. For example, snowshoe hare densities (and therefore biomasses) were similar in the spring estimates of 1993 and 1994, but the autumn estimates of 1992, 1993, and 1994 varied considerably from one another.

Finally, given the drama of the snowshoe hare cycle, we explore models of simpler food webs to determine how integral snowshoe hares and other species are to the dynamics observed. We examine models with hares as the only herbivores together with three abundant and cyclic predators. We also explore models in which snowshoe hares are excluded. The results from these reduced-web models should indicate how robust the model outputs of plant offtake and mass balance are to the presence of snowshoe hares, rare and noncyclic predators, and alternative prey species.

19.2 Modeling the Kluane System

To address these five questions, we used a series of four core models that we compared to each other and to the specialized models (table 19.1). The core models use herbivore data from control sites, typically averaged from all control sites that were studied for each species. These core models and most of the specialized models were run using autumn to autumn time periods because the autumn models start immediately after the production of the summer, therefore beginning at the annual maximum in biomass.

To address the impacts of food addition (+ food), we constructed four models, one for each of the four cyclic phases. Similarly, for predator reduction (− predator), we constructed models for each phase. For these treatment models, we varied ground squirrel and hare parameters but kept the other herbivore parameters the same as in the comparable control models. Doing this allowed us to focus on the species that were most impacted demographically by the experimental manipulations. To address seasonality, we constructed a control model that ran from spring to spring instead of from autumn to autumn for each cyclic phase.

Finally, we constructed two types of models of partial food webs using control data. In the first, we excluded all vertebrates except hares, lynx, coyotes, and great horned owls (minimum web models). The cyclic fluctuation of hares dominates the ecosystem dynamics of the boreal forest, and these three predators are all year-round residents that have hares as a dominant part of their diet. We considered including ground squirrels because they were typically the second-largest component of herbivore biomass and they were responsive both to the hare cycle and to the experimental treatments. But whereas hare cycles occur continentally throughout the boreal and sub-boreal forests of North America, ground squirrels are present in boreal forests only in the relatively small region of northern British Columbia, southern Yukon, and a small portion of Alaska. These stripped-down control models therefore are representative of the "typical" cyclic boreal forest species. The second set of partial web models excluded snowshoe hares but retained all other vertebrates as in the control full-web models (no-hare web models).

Because the experimental manipulations were not large enough to affect predator demography, we used the same year-specific values for raptors (goshawks, great horned owls) and mammalian predators (lynx, coyotes) in all models. For snowshoe hares and ground squirrels, both of which showed clear population cycles, we used both treatment- and year-specific variables. For the other herbivorous species and for Harlan's hawks and northern harriers, we used long-term averages because these species were more constant year-to-year (red squirrels, small birds, both raptors), rare (spruce grouse), or had unpredictable dynamics (small rodents).

19.3 Methods for Constructing Mass Balance Models

To construct and analyze mass balance models of the Kluane food web, we used Ecopath, a Windows-based software program developed at the International Center for Living Aquatic Resources Management, based on the original model by Polovina (1984)

Table 19.1 The models constructed for exploring vertebrate trophic interactions at Kluane.

Model	Variable Addressed	Difference from Core Model
Core Models		
Control peak (autumn 1988–89)	Cyclic phase	—
Control decline (autumn 1990–91)	Cyclic phase	—
Control low (autumn 1992–93)	Cyclic phase	—
Control increase (autumn 1994–95)	Cyclic phase	—
Specialized Models		
Spring peak (1989–90)	Season	Beginning season
Spring decline (1991–92)	Season	Beginning season
Spring low (1993–94)	Season	Beginning season
Spring increase (1995–96)	Season	Beginning season
+Food peak	Food	Hare and ground squirrel biomass, production
+Food decline	Food	Hare and ground squirrel biomass, production
+Food low	Food	Hare and ground squirrel biomass, production
+Food increase	Food	Hare and ground squirrel biomass, production
−Predator peak	Predators	Hare biomass, ground squirrel biomass and production, no lynx or coyote
−Predator decline	Predators	Hare biomass, ground squirrel biomass and production, no lynx or coyote
−Predator low	Predators	Hare biomass, ground squirrel biomass and production, no lynx or coyote
−Predator increase	Predators	Hare biomass, ground squirrel biomass and production, no lynx or coyote
Minimum food web peak	Trophic complexity	Only hare, lynx, coyote, great horned owl
Minimum food web decline	Trophic complexity	Only hare, lynx, coyote, great horned owl
Minimum food web low	Trophic complexity	Only hare, lynx, coyote, great horned owl
Minimum food web increase	Trophic complexity	Only hare, lynx, coyote, great horned owl
No-hare web peak	Trophic complexity	No hares
No-hare web decline	Trophic complexity	No hares
No-hare web low	Trophic complexity	No hares
No-hare web increase	Trophic complexity	No hares

All specialized models except the spring models were run from autumn to autumn of the years given for the core models.

(www.ecopath.org; Christensen and Pauly 1993, Pauly and Christensen 1995). Ecopath models require that four of five basic parameters be entered for each taxon. In general, biomass (*B*), production per biomass (*P/B*), consumption per biomass (*Q/B*), and diet composition are inputs, and matrix inversion algorithms in Ecopath determine the attendant ecotrophic efficiency (EE). These parameters are linked by the following equation:

$$B_r(P_r/B_r)(EE_r) = [\Sigma(B_c)(Q_c/B_c)(d_{rc})] + \Delta B_r, \qquad (1)$$

where *r* refers to parameters of the resource (species or guild), *c* to parameters of each consumer (species or guild), and d_{rc} is the proportion of *r* in the diet of *c*. Increases in resource biomass from one time to the next (bioaccumulation, or ΔB_r) can, along with consumption of the resource, be a fate for resource production.

The ecotrophic efficiency of a taxon compares the consumption and accumulation of biomass to the production of biomass. An $EE > 1$ indicates a problem: more consumption and bioaccumulation is occurring than is biologically possible given the production. High EE values therefore indicate either that the standing biomass is declining or that the model is an inadequate representation of the system. In our models, we initially included biomass increases (as a fate of production) but not biomass declines. For taxa showing biomass declines that also have $EE > 1$, we can then determine whether the excess consumption matches the empirically observed declines in biomass. An $EE \cong 1$ indicates that a species' dynamics are largely driven by consumption, whereas low values of EE indicate that production has a greater impact on the dynamics. When $EE < 1$, there is more production than bioaccumulation and consumption combined; this excess is assumed to become detritus. Low EEs therefore suggest potential for population increase because little of the production is being used in other parts of the food web.

We modeled the plant–herbivore interactions simplistically. We assumed that all herbivores ate from the same stock of plant material. To estimate offtake, we set $EE = 1$ for plants so that total consumption would equal production; we then set plant production equal to the standing stock. Ecopath solved for standing stock, thus generating our estimate of offtake.

Sources for demographic and trophic information about the Kluane boreal forest ecosystem include published studies and, whenever possible, data presented in previous chapters of this book. The species and interactions we modeled are shown in figure 19.3. General sources for demographic and dietary parameter values can be found in table 19.2. Below, we outline the transformations required to fit the demographic and dietary data into the mass balance ecosystem models.

19.3.1 Parameterization of Mass Balance Models

Biomass Density estimates were transformed from number per area into biomass per area by multiplying density and individual body mass for each taxon. For all taxa except hares and ground squirrels, these body masses were assumed to be constant throughout the cycle and for all treatments. Our density estimates of the different species come from different time periods throughout the year because density estimates were made at biologically relevant times for each species. We used separate autumn and spring estimates for hares and ground squirrels for each year. Ground squirrel densities were uncertain be-

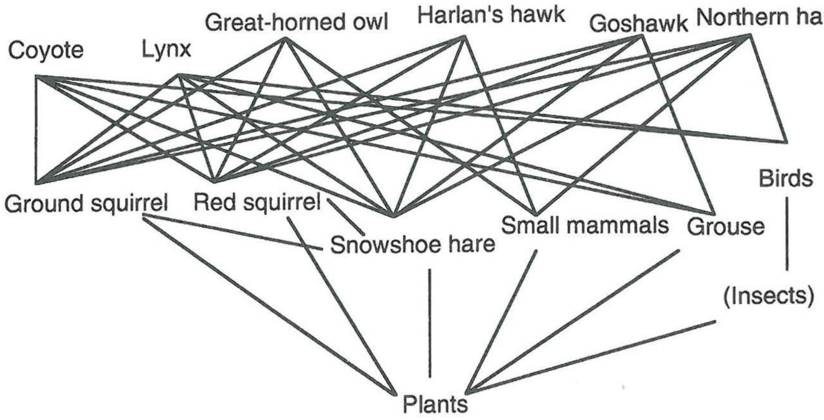

Figure 19.3 Taxa in the Kluane boreal forest food web that were included in the Ecopath models. Lines show dominant trophic relationships (>1% of the diet). Small mammals include *Microtus* and *Clethrionomys* voles. Birds include common small passerines, excluding woodpeckers and corvids. Many birds consume insects, but we did not model this interaction. Instead, birds were modeled as feeding directly on plants.

fore 1991 because of a different trapping regime (T. Karels personal communication), so we used spring 1991 densities for all prior models. Red squirrel numbers showed little variation among years, but autumn densities always exceeded spring densities due to reproduction during the summer, so we calculated average autumn and spring densities separately. For cyclic mammalian and avian predators (lynx, coyote, great horned owl, goshawk), the winter or spring densities were used in models for that spring and for the previous autumn. For example, coyote densities estimated from autumn 1989 to spring 1990 were applied to 1990 spring and 1989 autumn models. Similarly, great horned owl spring estimates were applied to that spring and to the previous autumn. For all other taxa, we used average densities based on all available density estimates from autumn 1988 to spring 1996 inclusive because coefficients of variation were small or because abundances changed erratically.

For models of the food-addition and predator-reduction treatments, we changed the biomasses of only hares and ground squirrels. Other herbivores did not respond to these treatments. For food-addition treatments, predator densities and biomasses were assumed to be the same as for controls because the experimental scale was smaller than the scale of predators' movements. To mimic the predator exclosure treatment, we excluded lynx and coyotes from the models but retained avian predators. For all species, bioaccumulation was calculated as the difference in biomass between years for biomass increases. Biomass losses between years were not incorporated into models initially.

Diet Composition The proportion of various prey items in the diet of each predator varied throughout the cycle. We estimated mammalian diets from scat analysis, with winter

Table 19.2 Data sources for the models.

Species	Demography	Intake rate	Diet
Snowshoe hare (chapter 8)	Krebs et al. 1995 Stefan 1998 Gillis 1998 O'Donoghue 1994 O'Donoghue and Krebs 1992 Hodges et al. 1999 Krebs et al. unpublished data	Pease et al. 1979* Hodges unpublished data	—
Ground squirrel (chapter 9)	Hubbs and Boonstra 1997 Karels et al. 2000 Karels et al. unpublished data	Nagy 1987*	O'Donoghue 1994 Stefan 1998
Red squirrel (chapter 9)	Boutin et al. unpublished data	Nagy 1987*	O'Donoghue 1994 Stefan 1998
Small mammals[a] (chapter 10)	Boonstra et al. unpublished data Krebs and Wingate 1985	Nagy 1987*	—
Spruce grouse (chapter 11)	Martin et al. unpublished data	Nagy 1987*	—
Small birds[b]	Folkard and Smith 1995 Smith unpublished data	Nagy 1987*	—
Lynx (chapter 13)	O'Donoghue et al. 1997 O'Donoghue unpublished data Slough and Mowat 1996*	O'Donoghue et al. 1998	O'Donoghue et al. 1998 O'Donoghue et al. unpublished data
Coyote (chapter 13)	O'Donoghue et al. 1997 O'Donoghue unpublished data	O'Donoghue et al. 1998	O'Donoghue et al. 1998 O'Donoghue et al. unpublished data
Great horned owl (chapter 15)	Rohner 1996 Doyle unpublished data	Nagy 1987*	Rohner 1994, 1996 Doyle unpublished data
Goshawk (chapter 16)	Doyle and Smith 1994 Doyle unpublished data	Nagy 1987*	Doyle unpublished data
Harlan's hawk (chapter 16)	Doyle unpublished data	Nagy 1987*	Doyle unpublished data
Northern harrier (chapter 16)	Doyle unpublished data	Nagy 1987*	Doyle unpublished data

For each species, many of the data are summarized in chapters in this book. A more detailed breakdown of the collated data is available by contacting the chapter authors, as is a complete description of how the demographic data were transformed into the model inputs. Asterisks denote non-Kluane sources. Herbivore diets were not modeled in detail, but the predation of red squirrels and ground squirrels on snowshoe hare leverets was included.

[a] The small mammal category includes the *Microtus* and *Clethrionomys* voles caught at Kluane.

[b] The small bird category includes the 10 most common passerine bird species (excluding corvids and woodpeckers) at Kluane, as described in Folkard and Smith (1995).

diets contributing two-thirds and summer diets one-third to the total diet. Diets of goshawks, Harlan's hawks, and northern harriers were calculated from items found in nests, and we assumed that adults were provisioning young with prey items similar to those they were eating themselves. Great horned owl diet estimates were based on items found in pellets and from prey remains at nests. Most great horned owl data are available for summer diets, which we use as half of the annual diet composition. About 90% of the biomass in the winter diets of great horned owls consists of hares (Rohner 1996), and we assumed the remainder was divided equally between small mammals and red squirrels. The number of individuals of each species was converted to proportion of biomass using a constant body mass for each prey item. Juvenile hares were assigned a biomass of 0.7 kg and leverets a biomass of 0.1 kg because most deaths occur within 5 days of birth (O'Donoghue 1994). We assumed diet composition to be constant across treatments.

Red squirrels and ground squirrels depredated hare leverets <2 weeks old. Although both red squirrels and ground squirrels are primarily herbivorous, we modeled the hares in their diet as well. We calculated kilograms hares consumed per kilogram squirrel annually as

$$C_{Lp} = \frac{L(1 - S_L)(M_{Lp} b_L)}{B_p}, \tag{2}$$

where C_{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 mass of a single leveret (0.1 kg), and B_p is total squirrel biomass. We calculated squirrel consumption of leverets separately for ground squirrels and red squirrels. To assign this consumption of leverets to a proportion of each squirrel species' diet, we calculated total consumption rate as described below.

Consumption per Biomass (Q/B) Daily energy needs for most taxa were calculated from Nagy's (1987) allometric relationships between body mass and consumption rate. He calculated separate relationships for birds, mammalian herbivores, and mammalian predators based on data from field studies and representing energy needs of active animals (e.g., animals that are foraging, moving, and thermoregulating).

Energy needs were calculated as kilocalories per kilogram per year. The amount of biomass required to meet these energy needs depends on the energy content of food (which varies with water, fat, and ash) and the consumer's efficiency of use. We assumed an assimilation efficiency of 80% of ingested energy, and energy contents of 1.75 kcal/g fresh weight (FW) for animals and 1 kcal/g for plants. Based on feeding by captive coyotes, metabolizable energy in snowshoe hares was measured directly as 1.4 kcal/g FW (Litvaitis and Mautz 1980), which is equivalent to 80% of 1.75 kcal/g. Feeding rates of migratory avian predators and songbirds were reduced to one-third because these species reside at Kluane for 4 months of the year. Similarly, ground squirrel feeding rates were reduced to one-third because of their winter hibernation.

These allometric estimates of consumption matched independent field data (Pease et al. 1979) and expert opinions on feeding rates of hares and avian predators at Kluane. However, rates at which snowshoe hares were killed by lynx and coyotes varied throughout the cycle, exceeding energy requirements at the peak but not at the low (O'Donoghue et al. 1998). We therefore used direct estimates of annual predation rates on hares for mammalian predators, weighted by the proportion of hares in the biomass of the diet. When we removed species from the models for the minimum food webs and no-hare webs, we altered diet compositions so that the remaining herbivores maintained their relative abundance in predators' diets.

Production per Biomass (P/B) Production per biomass generally represents total annual production over average biomass, but we used initial biomass for taxa that varied in biomass among years because we wanted to address biomass accumulation and loss. For taxa in which autumn and spring densities differed in the models, only individuals present in spring were allowed to contribute to production. For avian and mammalian predators, production was calculated as recruitment (R) of young into the adult population in units of individuals per individual (or kilograms per kilogram per year). This definition leaves out the production of offspring that died before adulthood (therefore $R \leq P/B$). For raptors,

$$R = rfn \tag{3}$$

and for lynx,

$$R = r[(Af_a n_a s_a) + (Yf_y n_y s_y)], \tag{4}$$

where R is recruitment, r is the proportion of females in the current population, f is the proportion of females breeding, n is litter size or young fledged, and s is survival until maturity. For lynx, yearling and adult reproductive parameters differed, so these were calculated separately, with A and Y representing the proportion of females in each age class (adult and yearling) and subscripts denoting the age-specific parameters. Birds were assumed to fledge at adult weight, and hence there was no need to incorporate a survival term. Coyote production was assumed to equal lynx production because we could find no data on coyote reproduction in boreal forests, and the temporal patterns in hunting group sizes of lynx and coyotes (an index of reproduction) at Kluane were similar (O'Donoghue et al. 1997). We calculated small mammal and grouse production (P/B) using similar equations. For small birds we set $P/B = 2$ because fledging rates should at least equal those of larger avian species.

For other herbivores, information was available on growth and mortality rates of young, which allowed us to include the biomass of young that did not reach adulthood into our production estimates. For ground squirrels and red squirrels, production was calculated taking into account the time it would take an emerging young to reach adult size:

$$P = drfn\left(b\int^{t} g \cdot e^{mt}\right) \tag{5}$$

where P is production, d is the spring breeding density, r is the proportion of females in the spring population, f is the proportion of females breeding, n is litter size, b is individual offspring mass at the starting time, g is the daily growth rate of young, m is the daily exponential mortality rate, and t is the time at which animals reach the next stage. For red squirrels and ground squirrels, we used equation 5 to calculate production from emergence to adult weight. To obtain production per biomass, this production is divided by either spring biomass or autumn biomass, depending on the season of the model. For ground squirrels, we used year-specific data for all parameters except size of emerging young (only 1993 data available). We also used year-specific birth, growth, and survival data for red squirrels, although interannual differences were not allowed to alter population densities, which were assumed to be invariant.

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

$$P = dr\sum f_L n_L (b_L + \int_0^{t1} g_L e^{m_L t_1} + \int_0^{t2} g_J e^{m_j t_2} \tag{6}$$

Variables are the same as in the production equation for squirrels, with L referring to the litter group (i.e., b_L, g_L, and m_L refer to the birth weight, growth rate, and mortality rate per litter group). Juvenile parameters (g_j, m_j) were assumed to be constant for all litter groups. We had juvenile survival data only for 1995–1996, so these values were applied to all years, whereas we used year-specific leveret parameters. 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 (i.e., 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 between litter groups 1 and 2, and growth rates of litters 3 and 4 were assumed to be intermediate between them (O'Donoghue and Krebs 1992).

We thus varied production for each taxon except grouse, small birds, and small mammals. For these taxa, interannual variation was small or we had limited or no year-by-year data. We therefore calculated average production for these taxa from the sources given in table 19.2. For hares, we varied production for the + food models by using data from food-addition treatments, but we used control values for the − predator models because we had no data on reproduction for the predator exclosure treatment, and hare-trapping records indicate that reproduction was probably similar to controls (Krebs et al. unpublished data). For ground squirrels, we varied reproductive parameters for both the + food and − predator models by using data from these treatments.

19.4 Results from Mass Balance Models

19.4.1 *Consumption of Plant Biomass by Herbivores*

Although we did not separate plants by species, a total biomass of between 10,000 and 40,000 kg/km^2 of consumed vegetation was estimated as necessary to support this food web (figure 19.4). Our estimates of plant consumption tracked hare densities through the cycle. Estimates of necessary plant biomass from autumn models were always higher than from spring models because consumption estimates were based on herbivore biomass present at the start of each model, and herbivore biomass was always higher in autumn than in spring because of summer production.

Estimated plant offtake was lower for reduced web models than for the control models because of lower herbivore biomass. The low phase estimate for the model with hares as the only herbivore was especially affected (figure 19.4a) because hares make up a much smaller proportion of herbivore biomass at this time than they do during the peak of the cycle (~65% of biomass at the peak and ~10% at the low; figure 19.1). In contrast, the low phase no-hare model showed little difference from the control model. Conversely, offtake differed most between no-hare and control models at the peak of the cycle (figure 19.4a), reflecting the high proportion of herbivore biomass composed of snowshoe hares at this time. Both the food addition and the predator exclosure treatments resulted in higher herbivore biomass (chapters 8, 9). In the models, this higher biomass translated into an increased offtake of plant biomass (figure 19.4b), a result also observed empirically (chapters 5, 6).

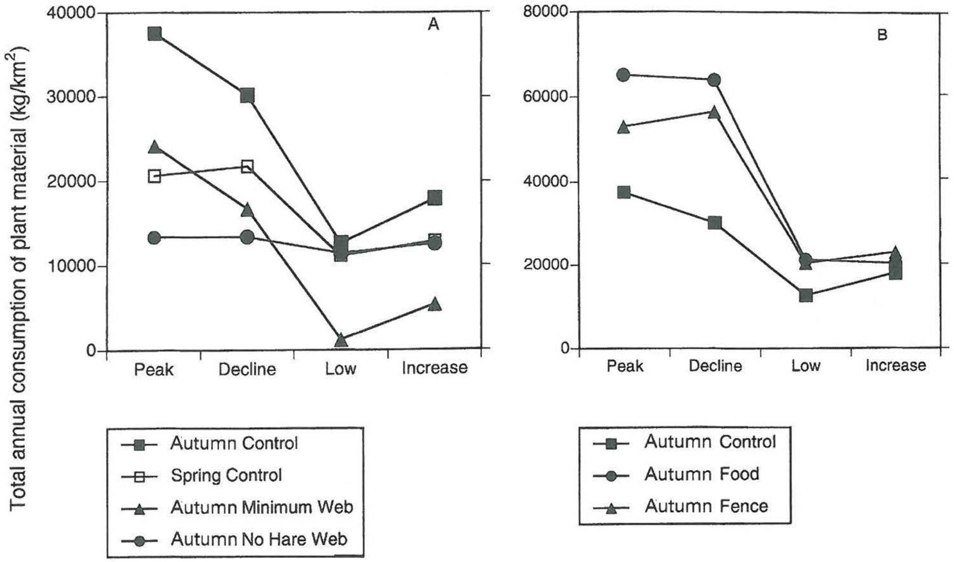

Figure 19.4 Plant biomass consumed by herbivores in Ecopath models of the Kluane boreal forest ecosystem. Feeding rates were calculated from allometric relationships of size versus energy needs for herbivores, assuming an energy content in plants of 1 kcal/g fresh weight. Energy needs of the total herbivore guild appear cyclic, which suggests that hare biomass is critical to total annual consumption. Each model was run for a year, with peak models starting in autumn 1988 and spring 1989; decline, autumn 1990 and spring 1991; low, autumn 1992 and spring 1993; increase, autumn 1994 and spring 1995. (a) Autumn, spring, and reduced web models. The minimum web model includes only plants, hares, and cyclic predators; the no-hare web excludes snowshoe hares while retaining all other modeled species. (b) Control, food addition, and predator reduction autumn models.

The Kluane experiments demonstrated changes in standing biomass of plants, with variation both in annual production (chapters 5, 6) and consumption (chapters 8, 9, 10, 11, 17). Estimates of offtake made via Ecopath ranged from roughly one-quarter to one-half of the standing crop of small (<5-mm diameter) birch and willow twigs (as estimated in chapter 6). However, not all herbivore consumption consists of twigs of these shrubs; boreal forest herbivores additionally eat shrub leaves, the needles, seeds, and twigs of spruce, fruits of various species, and forbs and grasses.

There was thus no obvious food limitation for herbivores. Additionally, our estimates of food offtake may well be high because energy content varies in different plant tissues and species; for instance, the spruce seeds consumed by red squirrels have much higher than our assumed 1 kcal/g FW (Rusch and Reeder 1978). Even so, there may be more subtle food limitations at work, such as the necessity for ground squirrels to obtain particular fatty acids required for hibernation (chapter 9), the reliance of red squirrels on spruce cone crops (chapter 9), and the nutritional versus defensive attributes of species and twig sizes for hares and grouse (Schmitz et al. 1992, Mueller 1993, Rodgers and Sinclair 1997). Modeling these interactions and addressing the relationships of plant growth and plant offtake through the cycle would require more detailed models.

19.4.2 Phase of Cycle Models

Hares Across phases, cyclic species showed dramatic fluctuations in EE, indicating shifts in the extent to which production kept pace with the known fates of biomass (figure 19.5). Ecotrophic efficiencies of hares were >1 during the decline and low phases, indicating insufficient production to account for the known consumption. In contrast, hares during the increase and peak phases had EEs < 1, which indicates that there was potential for even faster population growth than was observed; our models did not fully account for the fates of all the estimated hare production.

If more of a species' biomass is consumed than produced (i.e., EE > 1), the standing stock must decline. When we incorporated the decline in hare biomass as negative bioaccumulation into the autumn decline model, the resulting EE of hares changed from 1.67 to 0.98, indicating that the biomass flow balanced almost exactly when population losses were included and that the high initial EE was indeed associated with a population decline (figure 19.6). The EE was > 1 during the low phase as well. Part of this imbalance arises from a small amount of biomass accumulation; when consumption alone was considered as a fate of hare production, the EE dropped from 1.48 to 1.11. The model results show the importance of predators in causing the decline and in maintaining the low and mirror the experimental results that predation on hares was heavy during these phases (chapters 8,13,15).

The high hare EEs during the low phase indicate that predation has a heavy impact on hares in this phase. This predation effect occurred despite hare survival rates that were greater than during the decline (chapter 8) and the low but stable predator populations during the low phase (chapters 13, 14, 15, 16). The high EEs imply that predation may keep hares rare during the low phase, even though predators are scarce and have partially switched to feeding on other species (chapter 13). Typical models of the cycle have suggested that the low can be extended only if predators remain at high abundance for several years after the hare decline (Keith 1990). In contrast, our model results indicate that this delayed decline in predators is not necessary for predation to be the critical determinant of the duration of the low phase.

For snowshoe hares during the low phase, the high EE reveals a "predator pit" (Pech et al. 1995, Sinclair et al. 1998), in which a species is maintained at low densities by predators because offtake exceeds production. At low densities, hares on control areas simply could not produce quickly enough to swamp the ability of predators to consume the production. During the increase, hare production was slightly higher than during the low phase, partly through the presence of a fourth litter group and partly through an increase in hares weaned per litter (chapter 8; Stefan 1998), and these changes in production may have been just enough to allow hares to escape from the predator pit. We modeled the low phase on controls with increase phase production to see if that could allow hares to escape the predator pit. Doing so changed the EE from 1.11 to 0.73 (in the absence of biomass accumulation), which would allow population increase, thus confirming that the combination of low biomass and low production keeps hares in a predator pit.

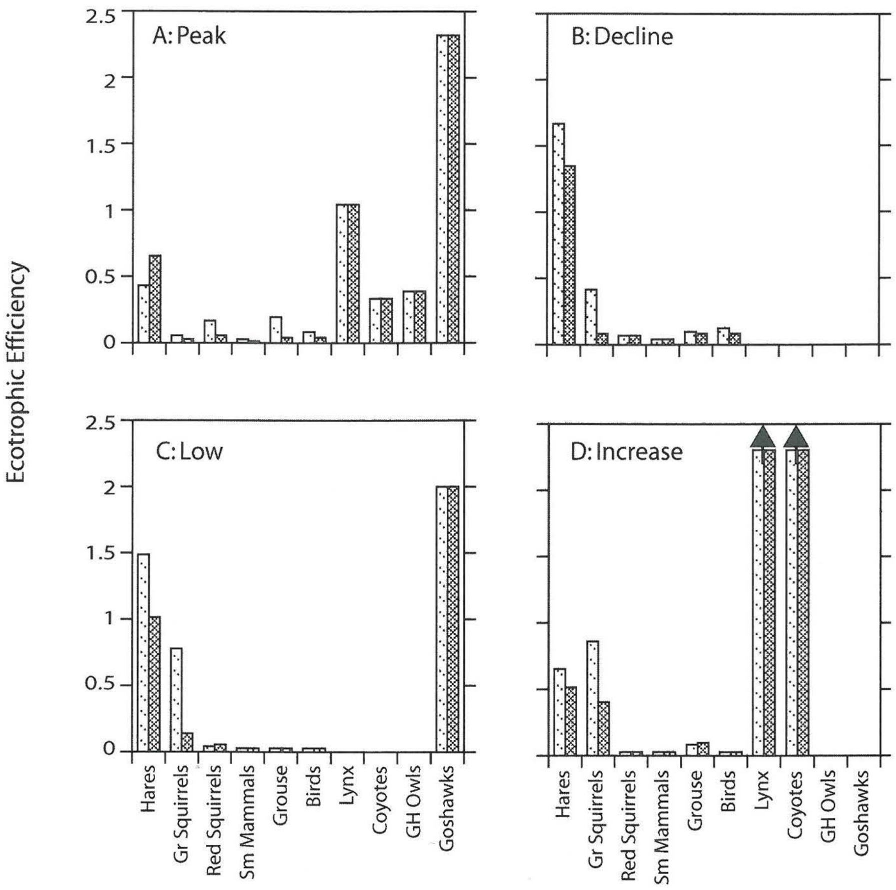

Figure 19.5 Ecotrophic efficiency (EE) of members of the Kluane boreal forest ecosystem. All animals in the model are shown except Harlan's hawks and northern harriers, which were assumed to be invariant year to year and therefore always had EE = 0. Other predators during the hare decline and low show EE = 0 because they had no biomass accumulation. Values of EE > 1 indicate that production cannot account for consumption by predators and for increased biomass. Model years are the same as in figure 19.4. In panel d, the arrows extending above the bars for lynx and coyotes indicate that their EE was infinite (population density increased in the absence of reproduction).

Based on biomass flows, some hare production had no known fate during the increase and peak phases (autumn EEs of 0.65 and 0.39, respectively). Ecotrophic efficiency was lower at the peak than during the increase phase, despite faster population growth rates during the increase phase. This pattern arises in part because biomass accumulation dur-

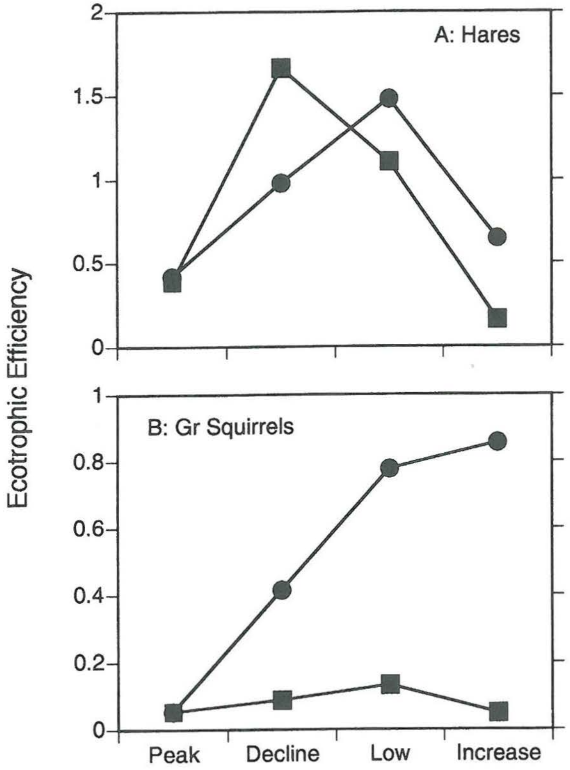

Figure 19.6 Ecotrophic efficiency (EE) of (a) hares and (b) ground squirrels based on Ecopath models that did (circles) or did not (squares) model changes in that species biomass. When circles < squares in terms of EE, biomass has declined. When circles > squares, biomass has increased. No biomass change was modeled for ground squirrels during the hare peak because density was not measured accurately before spring 1991.

ing the increase phase is included as a fate of production, thus increasing EE. When we removed the accumulation of biomass from the autumn increase phase model, hares went from an EE of 0.65 to 0.16 (figure 19.6). This low EE confirms that more production is available for population growth during the increase than at the peak.

The low EE values indicate that hares should have been able to increase even faster during the increase phase and should have been able to continue increasing during the population peak. Empirically, these patterns did not occur, which suggests that the models do not fully capture the system's dynamics. Artificially low EEs could arise if production was overestimated or if consumption was underestimated. Alternatively, low EEs could arise because of mortality sources other than predation (e.g., senescence or starvation), but starvation deaths of hares were rare at Kluane (chapter 8). We doubt that hare production was overestimated because, if anything, our methodology was likely to underestimate leveret survival. We suspect that our estimates of the feeding rates of predators were low for two reasons. First, we modeled predator consumption based on biomass of predators at the inception of the model year; predator production during that year would therefore not be applied to the consumption of hares. Second, we did not incorporate several of the smaller or rarer predator species, such as foxes, wolverine, eagles, boreal owls, and hawk owls. At Kluane, hawk owls appeared to display both functional and numerical responses to the hare cycle, with more birds present and a higher fraction of hares in the diet during the peak in hare densities (chapter 16; Rohner et al. 1995).

Studies in other locations have found functional or numerical responses to hares for some of these other predators as well (Theberge and Wedeles 1989, Dibello et al. 1990, McIntyre and Adams 1999). Our models included numerical responses of four predator species and functional responses of only coyotes and lynx. Clearly, including additional functional and numerical responses in the models would increase our estimates of hares consumed during the peak and could potentially raise EE to a level at which bioaccumulation would not be expected. These patterns raise the intriguing possibility that hares are limited at the peak of their cycle by rare and/or small predators, rather than by the major species that we have included in these food web models. Understanding predator functional responses may be critical to understanding the cycle.

Ground Squirrels and Other Herbivores Abundances of ground squirrels fluctuated in much the same pattern as did hares; however, this parallelism was not obvious in the 4 years we chose to represent phases of the cycle (figure 19.5). Our models had ground squirrels increasing in all phases except the peak (when we had no information on biomass change and therefore assumed constant biomass). When we eliminated bioaccumulation as a fate of production, ground squirrel EEs ranged from 0.05 to 0.13 (figure 19.6). The highest EE occurred during the low phase and probably reflects the fact that all predators except goshawks shifted their diet composition to include more ground squirrels as hare populations declined. Furthermore, ground squirrels have a known mortality source in addition to predation: approximately 40% suffer overwinter mortality during hibernation in their burrows (chapter 9). Given this mortality rate, an EE > 0.6 would indicate population decline. The observed EEs were still considerably lower than this value, but the impact of predation on ground squirrel populations may depend partly on the level of overwinter mortality.

The remainder of the herbivore guild had low and relatively constant EEs throughout the cycle (figure 19.5). These low EEs strongly indicate that the dynamics of these herbivores are not driven by predator–prey interactions; predators do not use a substantial proportion of their production. Experimental results support the conclusion that there is little top-down control of red squirrels, small mammals, small birds, and grouse (chapters 9, 10, 11, 12). Ecotrophic efficiencies of these herbivores were highest during the peak and decline phases. Comparing EE values of these species at the hare peak to the average of their three EE values for other phases indicates that during the hare peak red squirrels were consumed at 4.1 times their average rate and grouse at 2.8 times their average rate. During the hare decline, small mammals were consumed at 1.8 times their average rate and small birds at 2.8 times their average rate. During the decline, predator diets shifted away from hares and towards alternative prey, raising consumption of these species (chapter 13; O'Donoghue et al. 1998).

Predators During the decline and low phases of the hare cycle, many predators did not reproduce at all and abundances declined, thus leading to EEs of 0 (figure 19.5). During the increase phase, abundances of lynx and coyotes increased, but no reproduction occurred, giving effectively infinite EE. At the peak of the hare cycle, many predators increased in abundance, and these increases exceeded reproduction in lynx and in goshawks (EE $>$ 1). The excessively high EEs for lynx and coyote during the increase phase suggest that our models for these species need to be improved because recruitment did not match population increases. Two specific things would help: first, our production data for lynx were taken from elsewhere in Yukon (Slough and Mowat 1996), and our production data for coyotes were based on those for lynx because we could find no reproductive data for coyotes in boreal forests. Knowing the values for Kluane would almost certainly help. Second, unlike the herbivorous species at Kluane, lynx and coyotes are highly mobile (O'Donoghue et al. 1997, Poole 1997). The models as written do not incorporate movement into and out of the Shakwak Trench. If significant amounts of immigration occurred during the increase phase, then populations could increase in the absence of reproduction. For example, in 1994–1995, no reproduction was observed locally (based on observation of family groups; O'Donoghue et al. 1997), but biomass estimates rose from 0.24 to 0.35 kg/km^2 for lynx and from 0.20 to 0.23 kg/km^2 for coyotes. Such increases could have come about only through immigration. We explain the high EEs of goshawks during the low and increase phases in a similar fashion. These raptors occurred at low densities, were hard to census, and were also extremely mobile (chapter 16, Doyle and Smith 1994). Therefore the high EE values probably reflect immigration into the Shakwak Trench that we did not incorporate into our estimates of production. Alternatively, we may be seeing the consequences of error in population estimates.

19.4.3 *Seasonal Models*

Ecotrophic efficiencies of most species showed little difference whether models tracked populations from one autumn to the next or from spring to spring (figure 19.5). In part, this similarity reflects the identical parameters used for many species, because separate spring and autumn estimates were unavailable. Variation between autumn and spring models has two possible sources. First, small differences in ecotrophic efficiency arise due to shifts in diet composition of predators (e.g., predators ate proportionally more grouse in winter 1988–1989, applied to the peak autumn model, than in 1989–1990, applied to the peak spring model). Second, large differences in ecotrophic efficiency arise when biomass accumulation differs between autumn and spring (e.g., for the four years we examined, spring to spring biomass accumulation of hares exceeded autumn to autumn biomass accumulation only during the peak).

19.4.4 *Food Addition and Predator Reduction Models*

Both the addition of food and the reduction of predators resulted in dramatic differences in the ecotrophic efficiencies of herbivores (figure 19.7). Snowshoe hares had lower EEs on both treatments than on controls in all cyclic phases, with the exception of a higher EE for food addition treatments during the increase phase. The lower EEs of hares under

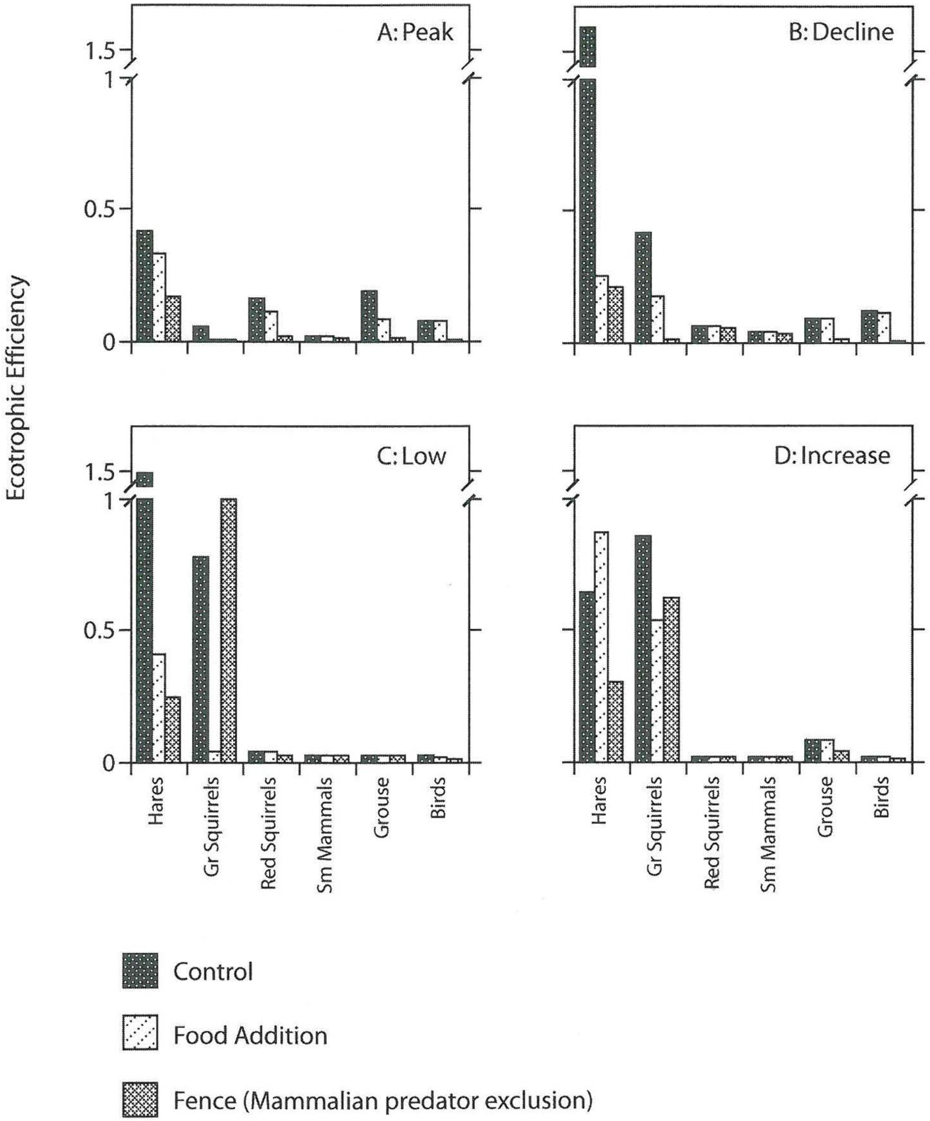

Figure 19.7 Treatment effects on ecotrophic efficiency of herbivores in the Kluane boreal forest ecosystem. Food models differ from control models in values for biomass and demography of hares and ground squirrels. The −predator models use hare and ground squirrel values from the site where mammalian predators were excluded; lynx and coyotes were not included in the model. Model years are as in figure 19.4.

treatment conditions in part reflect higher hare abundances on these treatments. For instance, at the peak, hare biomass was 343 kg/km^2 on control sites, 609 kg/km^2 on food addition sites, and 495 kg/km^2 on the predator exclosure treatment. Total hare production increases as a function of density because more individuals per area results in more offspring born per unit area, so both the food addition and predator exclosure treatments would have had higher hare production than did control sites. However, when we modeled consumption of this biomass on food treatments, we assumed it to be the same as on control areas. That is, predators were assumed neither to aggregate nor to feed at a higher rate when hare densities were high. Thus, consumption per production is reduced for the food-addition treatment, leading to lower EEs. On the predator exclosure, higher biomass of hares contributed to higher total production and, furthermore, lynx and coyotes removed no production, so EEs of hares dropped even further below those of controls. Theoretically, the low EEs on both treatments could be due to increased production by hares (on a per capita or per biomass basis), but our empirical results do not support this idea (chapter 8), so we suspect the EE differences are indeed due to the underlying biomass differences among treatments.

The low EEs for hares on treatment grids indicate that their dynamics were not predator limited; instead, their population dynamics were more responsive to initial biomass and cyclic changes in production. During the low phase, the extremely high control EE relative to the low EEs of the treatments reflects this difference in their initial biomasses. An exception to the general pattern of lower EE in treatment than control models occurs during the increase phase. The higher EE for the food-addition treatment may reflect the attraction of hares to the food-supplemented sites (chapter 8), thus augmenting abundance beyond the level expected from in situ reproduction. Similarly, population declines on treatment grids occurred despite low calculated values for EE. These declines could be partially due to movement of hares off the grids (chapter 8); because EE does not include movement as a potential fate, this could lead to low values of EE. Either directed movement from high to low density or random dispersal would tend to equalize abundances across treatments and would lower EEs for experimental sites.

Ground squirrels also had higher abundances on the food addition and predator exclosure areas than on control sites. Their EEs were accordingly lower for most treatment models than for control models. The exception (predator exclosure during the low) was a time of particularly high population growth (chapter 9), so this high EE actually reflects high biomass accumulation rather than high predator consumption.

Ecotrophic efficiencies of herbivores such as red squirrels, voles, grouse, and small birds were more affected by exclusion of mammalian predators than by addition of food. Food addition left EEs essentially unchanged, because these species did not respond demographically to the rabbit chow, and the predators were modeled identically to the controls. The slight variations between control and food-addition models arise because the body mass of hares and ground squirrels varied among treatments, and these values were used in calculations of mammalian predator consumption rates and diet composition of all predators, which in turn affects consumption of all herbivores by predators.

In contrast, the exclusion of mammalian predators had substantial effects on EEs of these other herbivores, especially during the cyclic peak. For all of these species, EE dropped sharply from control to − predator conditions when predators were abundant. This pattern indicates that the predator exclosure treatment reduced predation on red squirrels, grouse, small birds, and small mammals when predator densities were high. The predator exclosure treatment did not have this impact during the cyclic low phase. These patterns are explicable by considering the ways in which alternative prey can affect one another (Pech et al. 1995, Sinclair et al. 1998). In one scenario, high prey densities of one prey species (hares) can have a positive impact on other prey because the predators focus on the abundant prey. A diametrically opposed interaction could also occur, with high densities of one prey species leading to high predator densities, resulting in increasing predation on the alternative prey even if the predators' prey preferentially on the dominant prey species.

For grouse, red squirrels, small mammals, and small birds, it seems that the second interaction occurred. At high hare densities, these herbivores had lower EEs on the predator exclosure treatment. This suggests that lynx and coyote predation affected these alternative prey species during the hare peak, whereas the lack of impact of the predator exclosure treatment during the low phase suggests that lynx and coyote impacts were simply too low to affect these alternative prey. This result is somewhat counterintuitive because lynx and coyote diets changed to include a higher proportion of these alternative prey species during the cyclic low (chapter 13). Similarly, EEs for these herbivores in control models were highest when hare (and predator) densities were high, rather than when predator diets included relatively high proportions of alternative prey. These results therefore indicate that the dietary shifts of lynx and coyotes do not overcome their low densities sufficiently to impact the demography of alternative prey during the low phase.

19.4.5 Partial Food Web Models

The minimum food web included plants, hares, and the abundant cyclic predators (lynx, coyotes, great horned owl). The EE of hares changed little between the full and minimum food webs (figure 19.8). At the peak, the EE for hares was 15% lower when the other species were excluded (full: 0.394, minimum: 0.335). During the cyclic low, EE was 14% higher for the minimum food web model (full: 1.481, minimum: 1.685). These opposing effects indicate that during the peak the main effect of removing other species is reduced consumption of hares by predators (due to removing other predators), whereas during the decline and low the main effect of removing species is the lack of alternative prey, which causes the diet composition of the few remaining predators to consist exclusively of hares. Overall, the minimum food web with hares as the only herbivore and the three species of abundant cyclic predators did a remarkably good job of capturing the distinctive dynamics of the full boreal forest food web.

In contrast, trophic mass flows were substantially altered in models that left out hares relative to those including all taxa. In control models, most herbivores had EEs much lower than 0.1, but these values skyrocketed without hares because predators were modeled as consuming other species instead. The values of EE for herbivores neared or exceeded 1 when predators were abundant during the peak and decline phases. Taken together, these reduced web models reiterate the preeminent role that the snowshoe hare cycle plays in structuring the boreal forest food web.

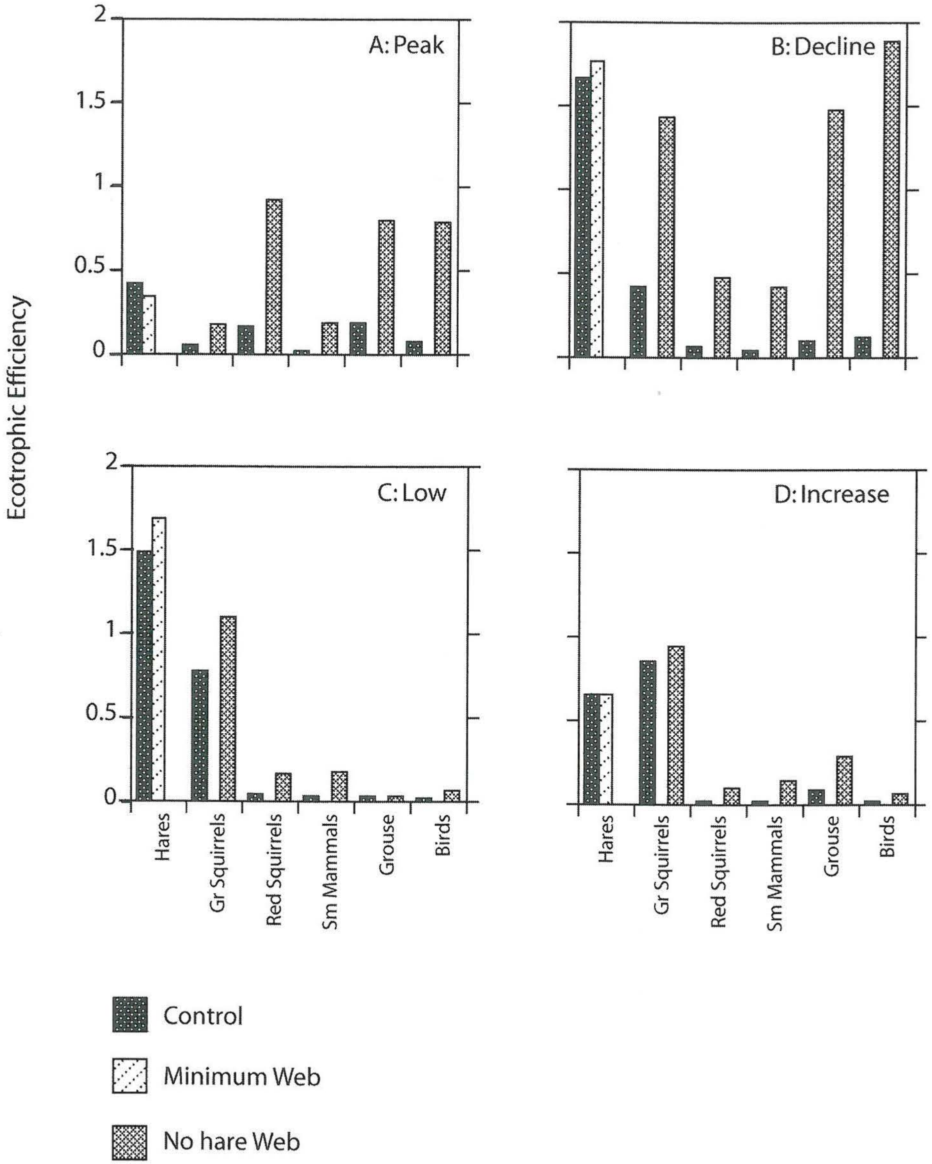

Figure 19.8 Ecotrophic efficiency of herbivores in the Kluane boreal forest ecosystem in control (full food web) models and reduced web models. The minimum web included plants, hares, coyotes, lynx, and great horned owls. The no-hare web differed from the full web only by the exclusion of hares. When some of a species' possible food sources were eliminated from a web, consumption was divided among remaining food sources according to their contribution to the diet. Model years are as in figure 19.4.

19.5 Discussion

19.5.1 *Do Predator–Prey Dynamics Structure the Boreal Forest Ecosystem?*

These mass balance models allow a way to contrast the impacts of food plants and predators on trophic interactions. As modeled, top-down effects of predators appear to be more important than bottom-up effects of food supply on the cyclic dynamics of hares. Consumption of hare biomass regularly exceeded production, whereas food plant biomass never appeared to be limiting. However, the food supply was not modeled in detail, and poor-quality food or absence of particular food types potentially could be responsible for the observed changes in per capita reproduction by hares.

Ecotrophic efficiency can serve as a proxy indicator of the strength of top-down interactions. When EE $>$ 1 (in the absence of bioaccumulation, which also raises EE), consumption of a species exceeds its production, and biomass should decline. This shift in biomass as a result of predation is one hallmark of a strong interaction (MacArthur 1972, Paine 1992). By this criterion, predators influence population dynamics of hares and perhaps ground squirrels (depending on how much the population is additionally reduced by overwinter hibernation mortality). Predators do not appear to influence population dynamics of other herbivores, despite some shifts in EE of these species through the cycle.

Predator–prey interactions may extend the low phase of the hare cycle. During the low phase, hares are in a predator pit that they escape only when reproduction and starting biomass allow them to swamp the remaining predators. During the decline phase, predators prey on hares at a high rate, and this consumption is sufficient to account for the observed biomass decline. The Ecopath models do not, however, indicate that hares should reach peak biomass when they do, because EE $<$ 1 at the hare peak, indicating that population growth could still occur. Predation at the peak by rare predators or predators that respond functionally to the cycle may account for the switch from increase to decline. We did not model other predators such as fox, wolverine, and eagles, but these species have shown functional responses to the hare cycle (Theberge and Wedeles 1989, Dibello et al. 1990, McIntyre and Adams 1999).

Predator–prey interactions may also cause ground squirrels to track the hare cycle in abundance. The high EEs for ground squirrels when predators are rare suggest that ground squirrels are an important alternative prey for predators during times of hare scarcity (see also chapter 9). Despite predators' heavier use of ground squirels when hares are scarce, hibernation limits their availability as alternative prey because they are below ground for 8 months of the year. Additionally, relatively high rates of overwinter mortality for ground squirrels (>40%) means that a substantial proportion of each year's production is unavailable to predators. Theoretically, ground squirrel EEs $>$ 0.6 could be associated with a predator-caused decline in biomass; the observed ground squirrel EEs were $<$0.15 in the core models developed here, which suggests that ground squirrels are probably not strongly predator limited.

Low EEs for most of the other herbivorous species (red squirrels, spruce grouse, small birds, and small mammals) suggest that they were primarily limited by food, weather, or space in the Kluane ecosystem. The predation impact did, however, increase when hare densities were high. The reduced web models show that omitting hares would drastically change the interaction of these species with the boreal forest predators by leading to much higher predation rates. Thus, these other herbivores are food limited only because the predators' attention is elsewhere. The hare–predator interaction dominates the food web structure in the boreal forest at Kluane.

These models explicitly incorporate only the direct effects of predation. Indirect effects may also occur. For example, the snowshoe hare predator pit during the low phase results from the interplay of predation pressure, hare biomass, and hare reproduction. If hares experience sublethal impacts of predation that affect their physiological capacity for reproduction, as has been suggested (Hik 1995, Boonstra et al. 1998), these impacts could prolong the low phase even if hare biomass and predation pressure were at levels conducive for hare population growth. The predator pit dynamics could also occur even with maximum hare reproductive output if predation pressure were high enough (i.e., if predation pressure declined with a lag, as has been suggested for hare cycles in other locations; Keith 1990). Experimental results on the predator exclosure treatment did not, however, lead to an earlier increase. The failure of the predator exclosure to produce an earlier increase probably reflects dispersal of hares from that treatment (chapter 8).

19.5.2 Potential for Other Ecopath Models

The models in this chapter have allowed us to paint a picture of the vertebrate dynamics at Kluane with a very broad brush. At this large scale, there are several more obvious model types to explore, plant–herbivore interactions foremost among them. From the Kluane data, it may be possible to construct a series of models examining plant biomass changes in a species-specific manner. Furthermore, we included no dynamics for detritus, although changes in both plant and animal detritus would be expected through the cycle. Similarly, inclusion of more season–year combinations for the treatments could detail the cyclic EE changes among vertebrates in more depth. These models can summarize cyclic changes in demography (P/B) but do not reveal why they occur.

We suspect that an interesting second generation of models could be derived by devotees of individual species using this modeling system with a much finer-scaled approach. Ecopath does not incorporate any kind of error structure in its inputs. It could be valuable to spend time manipulating variables for a given species to see the sensitivity of that species' EE to changes in any given demographic or dietary parameter. For cases where EE > 1, determining the parameter space that lowers EE below 1 could give insights into cases where empirical estimates may be biased. As an example, most of our raptor dietary data were obtained during summer and may not represent winter accurately; modeling variations in diet would allow us to determine if we could come closer to actual balances in EE. As another alternative focusing on particular species, examining results from a per treatment-grid basis rather than from averages for each treatment could open the door to speculation on site and scale effects.

Overall, the general utility of these biomass flow models lies in their ability to summarize trophic interactions among multiple species in a common framework. The detailed demographic information for each species thus becomes valuable not only in itself, but also in its contribution to our understanding of the linkages among species and between trophic levels. In addition, these models may help to disentangle the types of demographic changes that enhance or reduce bottom-up and top-down interactions by pointing out the sensitivity of EE to particular demographic variables.

19.5.3 Synthesis and Implications

We derive several key points from this modeling exercise. First, the ability of the minimum food web models to capture similar EE values for snowshoe hares indicates the central role of snowshoe hares in the boreal forest ecosystem. It is stunning to be able to start with 12 vertebrate species, remove 5 prey species and 3 predator species, and still derive similar results from the remaining 4 species. The results from the no-hare model offer even more striking evidence that snowshoe hares are centrally important to dynamics in the boreal forest.

Second, hares appear to be in a predator pit during the low phase of the cycle. This pit could be a result of low survival of adults or young hares, low reproductive output, or high predation pressure. There is an increase in reproduction and leveret survival from the low to the increase, which is consistent with the idea that leveret and juvenile dynamics hold the key to escaping from the predator pit. The models cannot distinguish among the various hypotheses for why there is low productivity at this time.

Third, the hare peak as modeled here remains difficult to explain because estimated production exceeded estimated consumption of hares. This conundrum can be resolved if hares die for reasons other than predation or if the predation rate on hares is higher than we modeled. Our results from radio-collared hares (with most hares dying of predation) and the results of studies indicating functional and numerical responses of many predators that we did not model suggest that predation may be higher at the peak than is currently supposed.

Fourth, ground squirrel dynamics appear to be responsive to the predation that accompanies the hare cycle, but with a slight lag behind the hares in that squirrel EEs (not counting bioaccumulation) were highest during the low of the hare cycle.

Fifth, prey species such as small mammals, grouse, red squirrels, and small birds appear to be more affected by mammalian predation when hare densities are high than when they are low. This result is consistent with the idea that high predator density rather than predator diet composition is the main determinant of predator impact on these species. These prey species did not demonstrate responses to the food addition treatment, but it is difficult to distinguish whether their lack of response means that they are not food limited or that rabbit chow was not a suitable food supplement for them.

Sixth, although many of the dynamics of the system were captured by this analysis of production and consumption, some of the model imbalances indicate that animal movements were also important. For predators such as lynx and coyotes, immigration into the Shakwak Trench resulted in increased densities during the early increase phase despite the lack of reproduction. Furthermore, although we did not model rare species, some raptors appear to be present only ephemerally during the cycle (chapter 16). These predator movements indicate that some of the food web dynamics may be integrated across a large spatial scale. At the scale of our experimental manipulations, hares appeared to be attracted to the food-supplemented treatments, resulting in faster population growth than in situ production can explain. Similarly, during the decline phase, there was a high rate of hare dispersal from the predator exclosure treatment.

Finally, the seasonal and treatment models both showed that the starting biomass in the modeled system affected two important dynamics: the amount of plant material required to support the food web and the relative amounts of production and consumption of hares. Some of the differences among treatments in the ecotrophic efficiency of hares may have resulted from differences in herbivore biomass, rather than directly from the annual demographic differences of treatments versus controls. Starting treatments at different times of the cycle, or modeling such an approach, could indicate how much of the treatment impacts are due to this bioaccumulation.

19.6 Summary

Understanding the dynamics of multispecies systems remains one of the major challenges to ecology, particularly when these interactions occur in a nonequilibrium context. In this chapter, we have described the interactions of multiple taxa of the boreal forest food web at Kluane in the single framework of trophic biomass flows. The value in this approach lies in the unification of demographic data into a common currency. However, the framework cannot easily incorporate nontrophic interactions such as movements, nor have we addressed uncertainty and error in parameter estimates.

One central focus of the Kluane project was to identify the causes and consequences of the snowshoe hare cycle. These Ecopath models corroborate the central importance of hares to the boreal forest food web and indicate that the interplay of snowshoe hare production, standing biomass, and consumption is crucial to cyclic dynamics. The transition from increase to decline appears to be predator driven, whereas the extended low phase appears to occur because of a predator pit that is influenced by the low production of hares. Herbivores other than hares were not limited by predation, largely because the predator–hare interaction was so strong. Predators had larger impacts on alternative prey (other than ground squirrels) during the hare peak, when predators were abundant, than during the hare low when predators were scarce but shifted their diets to include more alternative prey species.

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