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Vertebrate Community Structure in the Boreal Forest

Modeling the Effects of Trophic Interaction

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Models of biological communities have employed two general approaches: structural analysis of communities based on food webs (e.g., Paine 1980, Pimm 1982, 1991, Cohen 1989) and mechanistic models based on analysis of trophic interactions (e.g., Caughley 1976, 1977, Fretwell 1977, Tilman 1982, see chapter 17). Although both approaches have been used to understand community organization, mechanistic models generally provide more insight into the forces that influence community stability (Tilman 1982, Lawton and McGarvin 1986). Analyses of changes in biomass and productivity associated with experimental perturbation of the boreal forest (described elsewhere in this book) were used to test the nature of trophic-level interactions in this ecosystem described in chapter 17. The effect of trophic-level interactions on community organization were interpreted in terms of the role top-down (predator control) and bottom-up (nutrient limitation) processes played in changing the biomass or productivity of given trophic levels. The emphasis this approach places on biomass and productivity changes subsumes the more specific influence that trophic mechanisms can have on the maintenance of the species complexes within different trophic levels. For example, the observation that predation significantly reduces the biomass of herbivores clearly indicates that top-down processes are an important influence on community dynamics in this ecosystem. What is less clear is the role predation may play in facilitating coexistence among herbivores.

18.1 Trophic Interaction and Species Coexistence

Simple mechanistic models predict that where two or more species compete for limiting resources, the species with the highest rate of resource consumption or with the ability to monopolize resource access will competitively exclude all others (Gause 1934). From this basic premise, most theoretical and empirical studies of multiple species coexisting in communities have focused on identifying the circumstances under which coexistence can occur (Anderson and Kikkawa 1986, Yodzis 1993). A range of mechanisms that facilitate coexistence in communities have been identified (Tilman 1982, Tilman and Pacala 1993). These mechanisms can be divided into those that invoke the effect of limiting agents (predators, pathogens or parasites) or those that invoke limiting resources. Limiting agents facilitate coexistence where the susceptibility of competitors to a limiting agent varies temporally or spatially (Connell 1983), or where the agent constrains the density of competitors below levels where the resources for which they compete become limiting (Schoener 1986, Tilman and Pacala 1993). Limiting resources facilitate coexistence where the rate at which they are supplied to each competing species varies spatially or temporally (Tilman 1982, Tilman and Pacala 1993). The relative influence of limiting agents and limiting resources on community structure and function reflect the relative influence of top-down and bottom-up processes.

A central theme of the research described in this book was that experimental perturbation of factors influencing the abundance of snowshoe hares (a keystone species in the boreal forest) would elucidate the relative influence top-down (predation) and bottom-up (food resources) processes had on the structure and stability of the vertebrate community inhabiting the boreal forest at Kluane (chapters 1, 3). The analyses described in chapter 17 focused on what these perturbations revealed about the relative importance of top-down and bottom-up processes for changes in biomass and productivity at different trophic levels.

In the boreal forest, vertebrates occupying at least two trophic levels (herbivores and carnivores) coexist despite potential competition for food resources. In this chapter we construct simple models of trophic interaction between some of the dominant species in the boreal forest to explore potential mechanisms of coexistence for herbivores and carnivores. In particular, we focus on coexistence of snowshoe hares and ground squirrels as potential competitors for summer vegetation, and of lynx, coyote, and great horned owls as competitors for available prey during the cyclic low in snowshoe hare abundance. Mechanisms of coexistence are interpreted in terms of the influence of the top-down and bottom-up influences described in chapter 17.

18.2 Interaction between Vegetation and Herbivores

Snowshoe hares and ground squirrels use some of the same food resources over summer. However, although this provides some potential for competition, exclusion of one or other species does not occur because (1) the food resources that limit snowshoe hare and ground squirrel populations are different, or (2) predation keeps the density of both species below levels where they compete for food resources. (A third possibility is that social regulation limits the density of both species below levels where they compete for food. However, there is little empirical evidence that either hares or ground squirrels are intrinsically regulated, and this hypothesis is not explored further in this chapter.) These hypotheses are not mutually exclusive. Predation may hold snowshoe hare and ground squirrel densities below certain levels where they are food limited, regardless of whether or not they compete for the same food resource. For example, the analyses described in chapter 17 suggest that herbivores in the boreal forest are influenced by the reciprocal effects of top-down and bottom-up processes, corresponding to the simultaneous or sequential influence of predation and food limitation.

The potential for competition between snowshoe hares and ground squirrels will largely depend on how food availability at different times of the year influences their demographic rates. During the time ground squirrels are active, they rely primarily on summer herbs for nutrition (chapter 9). When preferred herbs are unavailable, ground squirrels will consume grasses and willow, upon which adults can survive but not reproduce (T. Karels personal communication). Hence, in the absence of predation, the availability of summer herbs appears to limit ground squirrel populations. In contrast, snowshoe hares remain active year-round. Snowshoe hares rely on the terminal twigs of shrubs over winter but consume a range of forbs, grasses, and the leaves of shrubs during the summer (chapter 8). Although considerable work has been undertaken on winter feeding by snowshoe hares (chapter 8), summer feeding patterns are less well understood. Both severe browsing effects and mobilization of secondary plant compounds for shrubs over winter have been observed during the cyclic peak in snowshoe hare densities. This has led to the general assumption that any food limitation acting on snowshoe hare populations will be related to shrub availability over winter (Pease et al. 1979, Bryant 1981, Fox and Bryant 1984, Sinclair et al. 1988, Smith et al. 1988). However, in this study, although the biomass of terminal twigs showed a cyclic decline related to snowshoe hare browsing, there was no evidence that the general availability of winter food ever fell to levels that would limit reproduction or survival (chapter 8). Hence, in the absence of predation, it is not known whether shrubs over winter or herbs over summer would eventually limit snowshoe hare populations.

While bottom-up effects may be important for general patterns of variation in herbivore biomass, seasonal patterns in these effects may have important consequences for herbivore species composition. For example, because ground squirrels do not feed over winter, potential competition with snowshoe hares is largely restricted to consumption of herbs over summer. If the availability of shrubs had more influence on predation-free snowshoe hare populations than the availability of herbs, the scope for competition with ground squirrels would be limited. However, if the availability of summer herbs had more influence on predation-free snowshoe hare populations, the potential for competition with ground squirrels would be greater. To evaluate whether snowshoe hares and ground squirrels would persist in the absence of predation, we developed a model of their interaction with summer and winter food resources. If predation is necessary to facilitate coexistence of snowshoe hares and ground squirrels, in its absence we should be unable to maintain both herbivores within the modeled system.

18.3 Interaction between Herbivores and Predators

The three dominant predators in the boreal forest are lynx, coyote and great horned owls (chapters 13, 15). All three predators share snowshoe hares as their most common prey, and cyclic changes in the density and demography of these predators demonstrate that they are fundamentally limited by snowshoe hare abundance during the low-phase of the snowshoe hare cycle. Hence, the role bottom-up processes play in structuring the predator community in the boreal forest is self-evident. Similarly, the clear association between cyclic changes in the abundance of snowshoe hares and the demography of lynx, coyote, and great horned owls suggest that temporal rather than spatial variation in the rate at which snowshoe hares are supplied to these predators facilitates their coexistence. This implies that the increase in prey abundance following the low-phase of the snowshoe hare cycle must occur regularly enough (i.e., every 9–11 years) that lynx, coyote, and great horned owls avoid competitively excluding one another. The cyclic increase in snowshoe hare abundance appears necessary for predator coexistence, despite the diversification of predator diets during the low-phase of the snowshoe hare cycle. For example, although lynx were to some extent able to substitute alternative prey (especially red squirrels) when snowshoe hare availability was low (1992–1995; see chapter 13), the abundance of lynx continued to decline over this period. Hence, although predators could potentially reduce competition during the cyclic low-phase in snowshoe hare density by broadening their diet, they could not sufficiently alleviate the effect that low snowshoe hare availability had on their demography to halt their ongoing decline. It follows that if the low-phase of the snowshoe hare cycle were protracted, competition between these three predators would intensify, and their continuing coexistence would become less certain.

18.4 Modeling

The models described in this chapter are contained in a single Excel spreadsheet on the CD-ROM (frame 71, multiprey accounting model) that accompanies this book (Community.xls). The spreadsheet allows the structure of the model to be explored interactively and the scenarios described in this chapter to be set up and varied. Excel's accounting tools (which allow cell precedents and dependents to be traced) are particularly useful in tracking how constants and variables are related throughout these models.

All models ran for 100 years, with a basic time step of 6 months dividing each year into winter and summer periods. The abundance of all animal species could be switched between densities based on field estimates or densities predicted by the model.

18.4.1 Interaction between Vegetation and Herbivores

Models that linked the dynamics of snowshoe hares and ground squirrels to that of summer vegetation (herbs) and year-round vegetation (shrubs), used the functional and demographic responses of each herbivore to changes in herb and shrub biomass (figure 18.1). Both herbs and shrubs grew logistically, values for maximum instantaneous growth rate (herbs: 0.5, shrubs: 0.15) and biomass at carrying capacity (herbs: 200 kg/ha, shrubs: 1500 kg/ha) being selected to approximate seasonal productivities estimated in chapters 5 and 6 (figure 18.2). Herbs were available and grew only over the 6 months designated as summer. Shrubs also grew over summer but were available year-round.

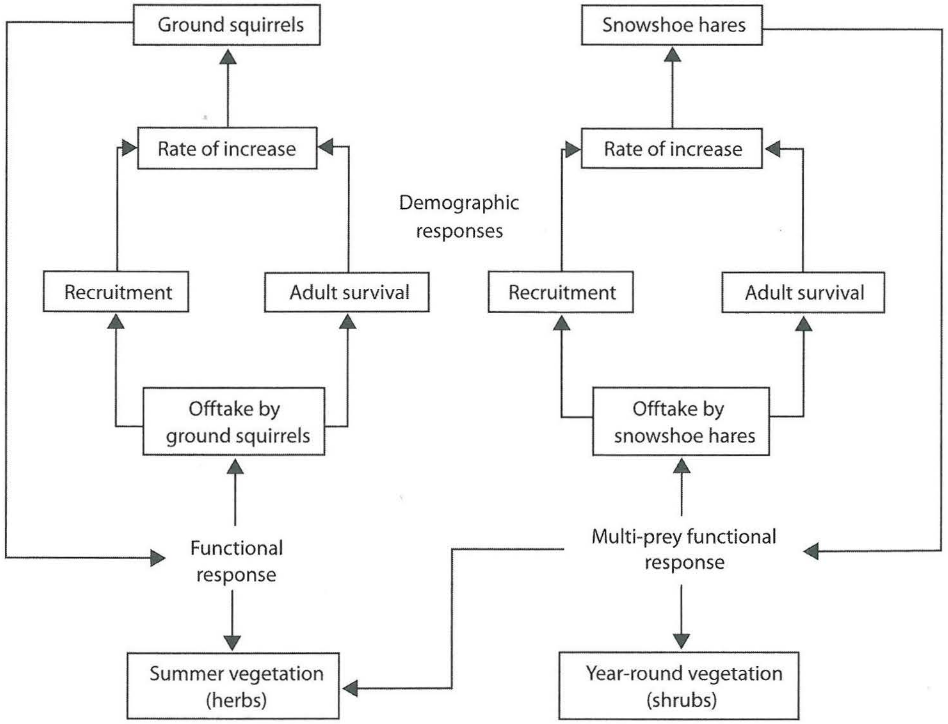

Figure 18.1 Structure of the model linking vegetation to snowshoe hare and ground squirrel population dynamics.

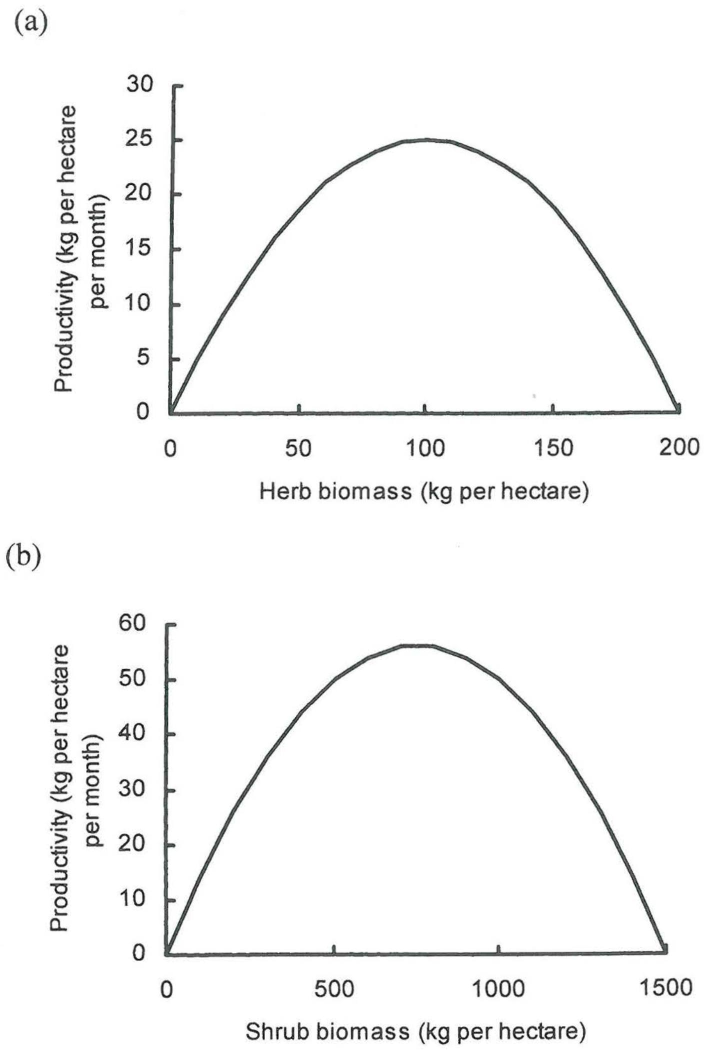

Figure 18.2 Productivity of (a) herbs and (b) shrubs as used in the model linking vegetation to snowshoe hare and ground squirrel population dynamics.

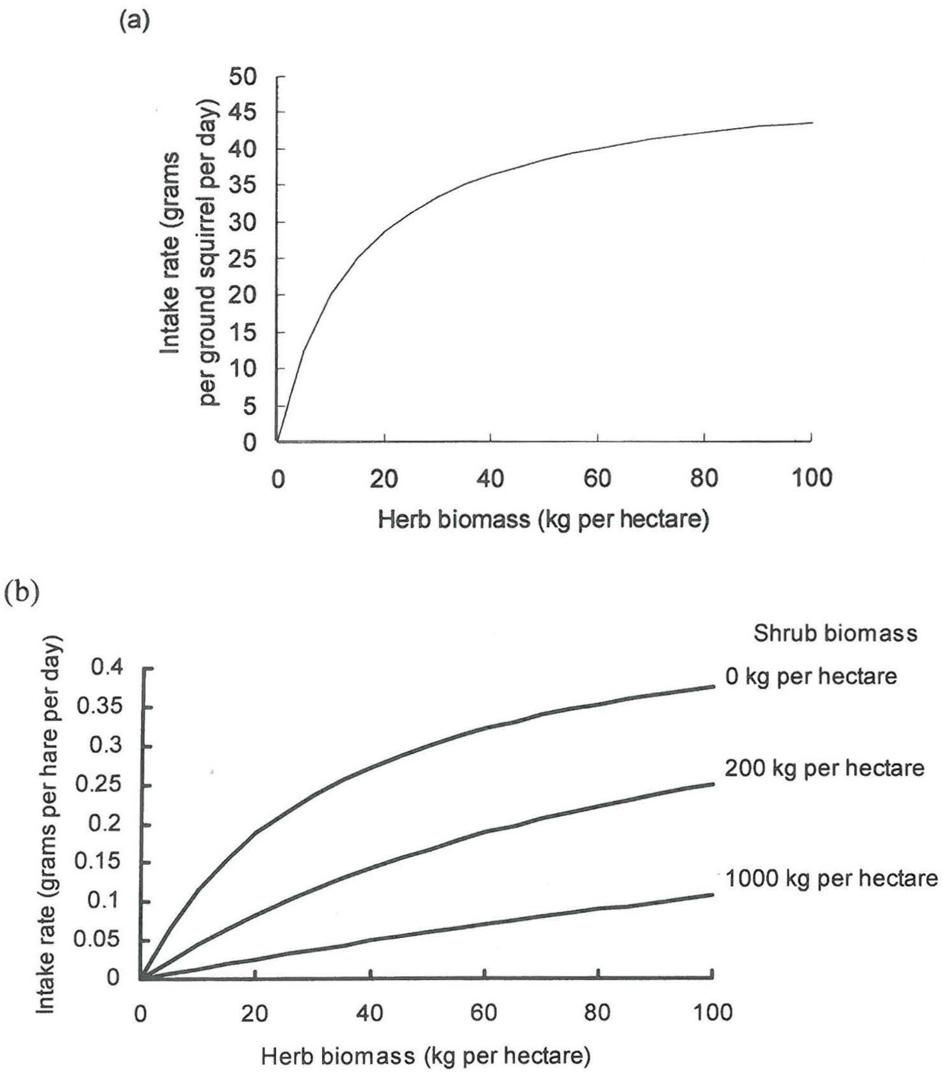

Figure 18.3 Functional responses of (a) ground squirrels and (b) snowshoe hares consuming summer herbs. The range of responses shown for snowshoe hares shows the effect of increasing shrub availability on herb offtake.

Ground squirrels consumed herbs only, with per capita offtake (I_s) being related to herb biomass (s) by a functional response described using Holling's (1959) disc equation (figure 18.3a):

$$l_s = \frac{(a_s s)}{1 + a_s h_s s)}, \tag{1}$$

where a_s is the rate of effective search of ground squirrels for herbs, and h_s is handling time, which is equal to the time each ground squirrel takes to consume and digest each kilogram of herbs it finds. Handling time was estimated as the reciprocal of maximum herb intake rate, which was assumed to be 0.3 kg per ground squirrel per day ($h_s = 3.33$). Rate of effective search was derived by using observed ground squirrel densities in the model, then varying a_s until a plausible pattern of variation in herb biomass was achieved. This gave a rate of effective search of $a_s = 0.02$.

Snowshoe hares consumed both herbs and shrubs, with respective offtake related to the instantaneous availability of each by functional responses described using a multiple-prey version of the disc equation (Caughley and Sinclair 1994; figure 18.3b). The functional responses for herbs and shrubs were:

$$l_s = \frac{(a_s h_s s)}{1+[(a_s h_s s)+(a_w h_w w)]} \tag{2}$$

and

$$l_w = \frac{(a_w h_w w)}{1+[(a_w h_w w)+(a_s h_s s)]}, \tag{3}$$

where a_s and a_w are the rates of effective search by snowshoe hares for herbs and shrubs, respectively, and h_s and h_w are the handling times, which are equal to the time taken to consume and digest each kilogram of herbs and shrubs found.

Schmitz et al. (1992) estimated maximum shrub intake by snowshoe hares at 0.5 kg per hare per day. It was assumed that maximum intake of herbs (i.e., the maximum intake of herbs if no shrubs were available) would be the same, giving a value of 2 for both h_s and h_w. As with rate of effective search for ground squirrels, a_s and a_w were derived by using observed snowshoe hare densities in the model, then varying each until plausible patterns of variation in herb and shrub biomass were achieved. This gave rates of effective search of $a_s = 0.015$ and $a_w = 0.005$. The relative values for rates of effective search by ground squirrels and snowshoe hares implies that ground squirrels are more efficient foragers for herbs than are snowshoe hares and that snowshoe hares forage more efficiently for herbs than they do for shrubs. Vegetation growth and offtake were accounted monthly for each sequential summer and winter phase (see the worksheets "Herbivore responses" and "Vegetation" of Community.xls on the CD-ROM for details).

We simulated the demography of both snowshoe hares and ground squirrels by linking variation in per capita recruitment (*R*) and adult survival (*S*) in the absence of predation to average food intake over each 6-month period. Average rate of food intake over each 6-month period was expressed as a proportion of maximum possible intake to calculate a food intake deficit. For both ground squirrels and snowshoe hares, recruitment and adult survival were related to food intake deficit using an exponential saturation curve that had the form:

$$D = D_{\max}(1 - e^{-FDd}), \tag{4}$$

where the demographic rate of interest is *D* (i.e., recruitment or adult survival), its maximum potential rate is $D_{\max}$, food intake deficit is *FD*, and *d* is a measure of demographic efficiency describing the relative effect a decline in food intake has on the demographic rate. The parameter measuring demographic efficiency is a unit-less index that simply controls how rapidly declining food intake rate reduces either recruitment or adult survival. As its value increases, any decrease in food intake (measured here as a change in food intake deficit) will have a less dramatic effect on recruitment or survival. As its value decreases, any decrease in food intake will have a more dramatic effect on recruitment or survival.

Variation in recruitment and adult survival with food intake deficit for snowshoe hares and ground squirrels is shown in figure 18.4a and b, respectively. Maximum recruitment for ground squirrels ($R_{\max} = 1.86$) was estimated from maximum litter size and weaning rates on the predator exclosure grid to exclude any indirect effects of predation on reproduction (chapter 9). Maximum adult survival for ground squirrels over summer was assumed to be high ($S_{\max} = 1$), given the low mortality unrelated to predation. Because overwinter survival of ground squirrels is independent of food availability, the variable summer rate was replaced with a constant rate estimated from field data ($D = 0.66$). We estimated maximum recruitment of snowshoe hares ($R_{\max} = 5.30$) from the product of maximum fecundity and maximum juvenile survival. Maximum adult survival for snowshoe hares year-round was assumed to be high ($S_{\max} = 0.9$), given low mortality unrelated to predation (chapter 8). Recruitment and adult survival over each sequential 6-month period of summer and winter were combined in an additive model that predicted instantaneous rates of change (*r*) in ground squirrel and snowshoe hare abundance (see

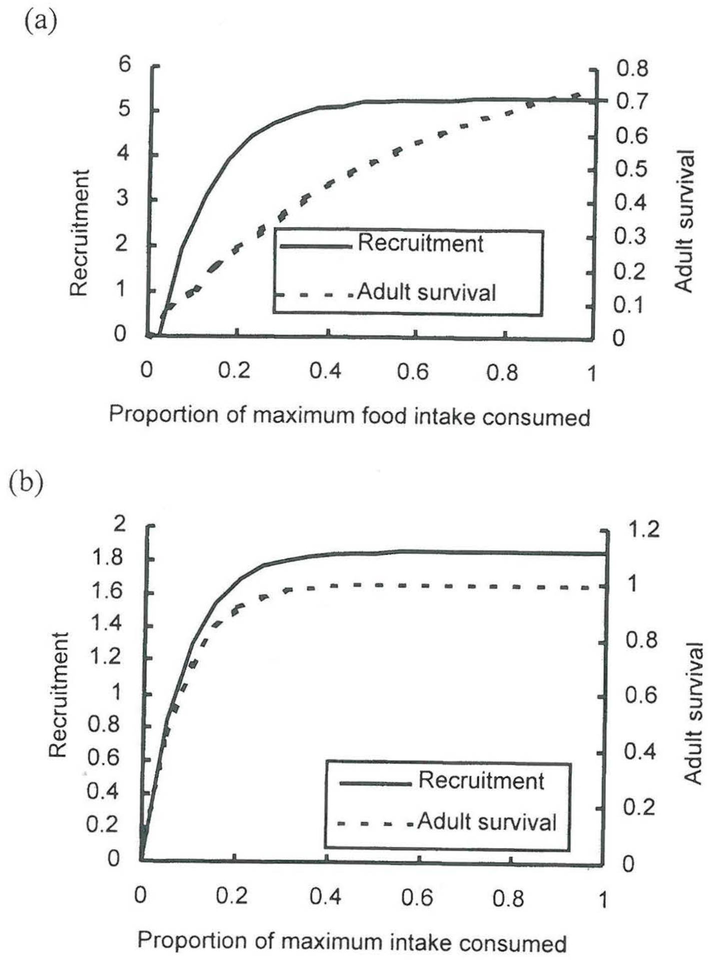

Figure 18.4 Demographic responses of (a) snowshoe hares and (b) ground squirrels with decreasing food intake deficit.

the worksheet "Herbivore responses" in Community.xls on the CD-ROM for additional details).

18.4.2 Equilibrium Conditions for Snowshoe Hares and Ground Squirrels

To determine whether it was possible for ground squirrels and snowshoe hares to persist indefinitely in the absence of predation (i.e., whether their food resources were sufficiently different to avoid competitive exclusion), we varied relative demographic efficiencies (*d* values for recruitment and adult survival) for each species independently and together, and changes in their respective densities and biomass of their food resources assessed. For each species, the relative efficiencies for recruitment and adult survival were interchangeable over a wide range of values. Hence, to explore equilibrium conditions for snowshoe hares, adult survival efficiency was set to 0.8 while recruitment efficiency was varied; and for ground squirrels, adult summer survival efficiency was set to 3 while recruitment efficiency was varied. By varying recruitment efficiencies for each species, the models changed the sensitivity of reproduction and juvenile survival (the product of which is recruitment) to fluctuations in food availability, such that declining food intake had a greater or lesser effect on rates of population change.

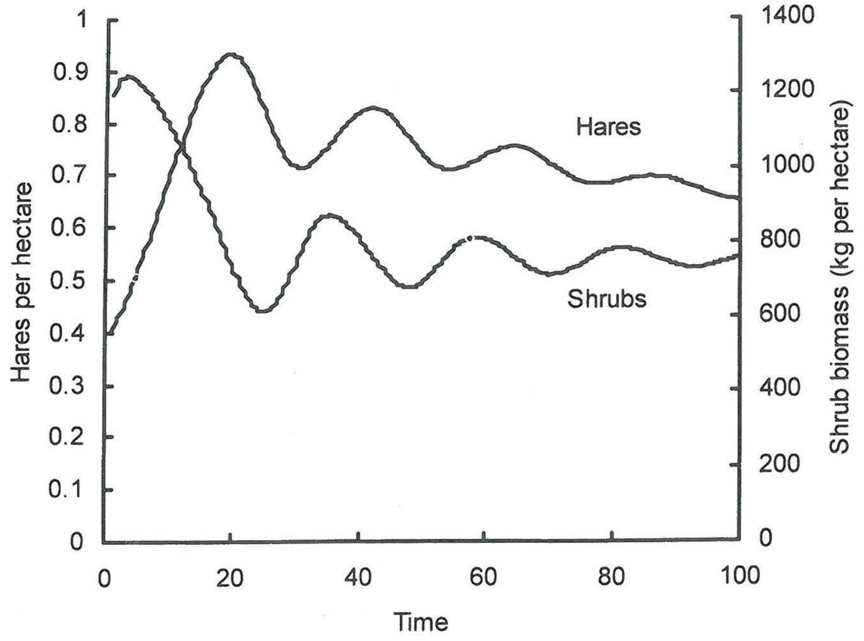

Figure 18.5 Reciprocal variation in snowshoe hares and shrubs when only hares are included in the model. Adult survival efficiency is set to 0.8 and recruitment efficiency to 2.5.

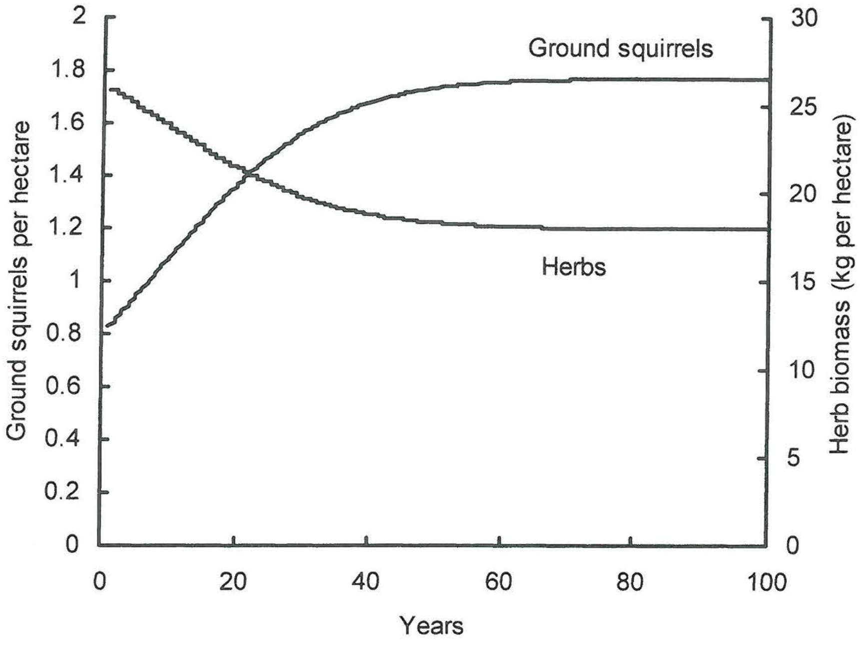

Figure 18.6 Reciprocal variation in ground squirrel and herbs when only ground squirrels are included in the model. Adult survival efficiency is set to 3 and recruitment efficiency to 4.

When snowshoe hares were modeled alone, recruitment efficiencies between 2 and 2.6 produced an equilibrium with food resources, the equilibrium being approached through dampening oscillations at higher values within this range (figure 18.5). At lower recruitment efficiencies, snowshoe hares underwent deterministic extinction, shrub biomass moved to a specified maximum, and herb biomass waxed and waned through the sequence of summers and winters. Between recruitment efficiencies of 2.7 and 3.3, snowshoe hares and their food resources became locked into stable limit cycles, the amplitude of cycles increasing with recruitment efficiency. Above a recruitment efficiency of 3.3, snowshoe hares underwent a sequence of increasing eruptions until their food resources collapsed and they crashed to extinction. The only stable scenarios in which snowshoe hares approached maximum densities seen on control and predator exclosure grids were those producing stable limit cycles of higher amplitude (i.e., those brought about by recruitment efficiencies >3).

When ground squirrels were modeled alone, all recruitment efficiencies >3 produced stable equilibria between squirrels and their food resources. The average density of equilibria increased with recruitment efficiency until efficiency exceeded 6, when ground squirrel density stabilized at an average of about 3/ha (figure 18.6). At recruitment efficiencies <3, ground squirrels underwent deterministic extinction.

When snowshoe hares and ground squirrels were modeled together, coexistence proved possible over a broad range of recruitment efficiencies. However, the range of efficiencies that produced stable outcomes was increased over those when the two species were modeled by themselves. For example, if ground recruitment efficiency for ground squirrels was set to 6.5, the range of efficiencies required for snowshoe hares to achieve some form of equilibrium with their food resources increased from 2–3.3 to 2.2–3.3. This

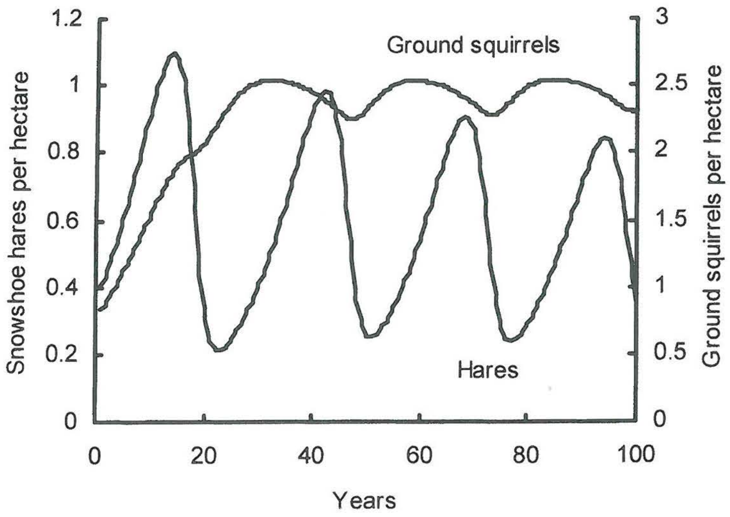

Figure 18.7 Variation in snowshoe hare and ground squirrel density when both are included in the model. Adult survival efficiencies are set to 0.8 and 3 for snowshoe hares and ground squirrels, respectively, and recruitment efficiencies to 3 and 6.6, respectively.

suggests that competition from ground squirrels for summer food resources required snowshoe hare populations to have higher net productivity than necessary for equilibrium in the absence of ground squirrels. Snowshoe hares had a reciprocal competitive effect on ground squirrels, their presence (at a recruitment efficiency of 3) pushing up the range of recruitment efficiencies ground squirrels require for equilibrium from values around 3 to 3.5. Evidence of competition for food resources can be seen in the reciprocal oscillation of snowshoe hares and ground squirrels over a broad range of recruitment efficiencies for both species (figure 18.7).

In the absence of predation, snowshoe hares and ground squirrels appear theoretically capable of coexisting, despite potential competition for summer food resources. Coexistence is consistent with the limiting food resources of each species being sufficiently different to avoid competitive exclusion. This implies that bottom-up processes not only influence herbivore biomass but may also be important for herbivore coexistence.

For example, the degree to which snowshoe hares and ground squirrels compete in these models is determined by the relative efficiency with which each species can use herbs to enhance rates of increase and the effect shrub availability has on the degree to which snowshoe hares will consume herbs as their biomass declines. We set foraging efficiencies in the model so that ground squirrels were better foragers for herbs than snowshoe hares, but so that snowshoe hares preferred herbs to shrubs when both were available. The capacity of snowshoe hares to use shrubs year-round effectively buffers this system from more intense competition between snowshoe hares and ground squirrels for herbs over summer. The effect of this buffering can be seen by reducing the maximum rate of shrub growth, forcing the two herbivores to compete more aggressively for summer food (figure 18.8). This reduces shrub productivity below levels that can sustain viable

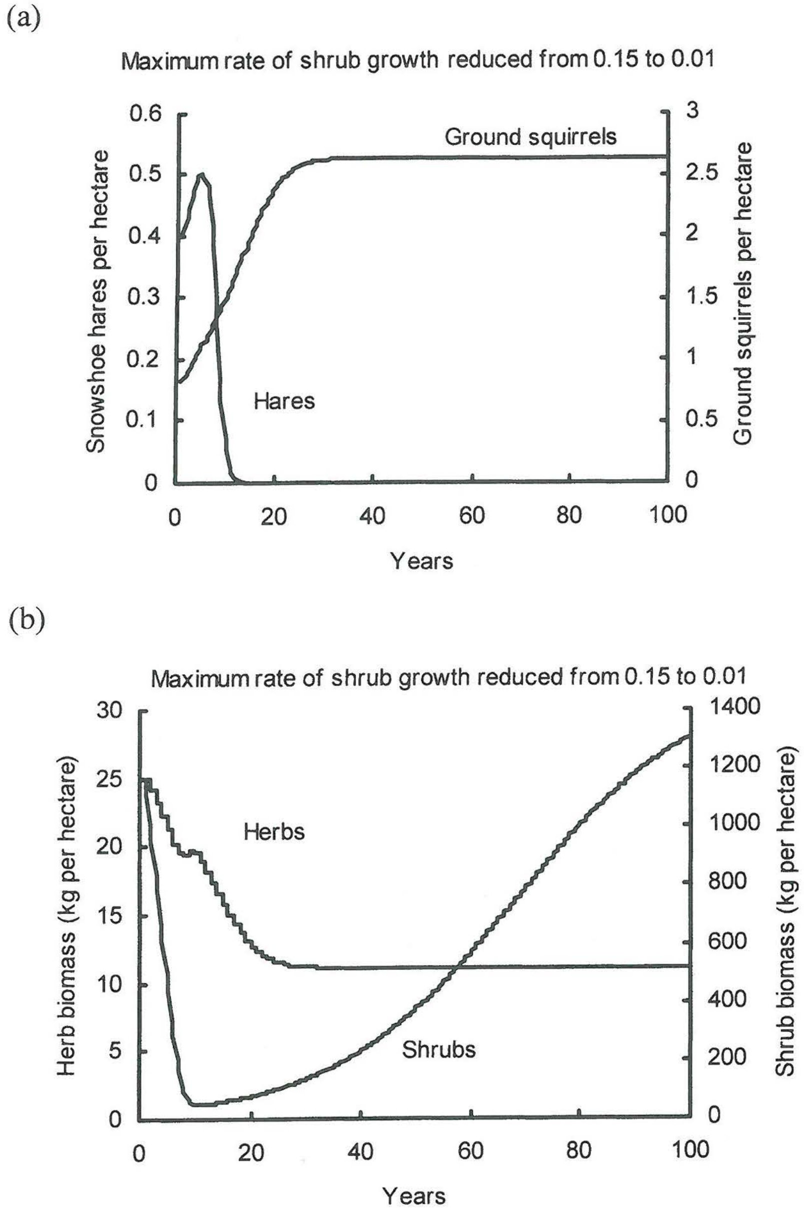

Figure 18.8 The effect of reducing the maximum rate of shrub growth on competition between snowshoe hares and ground squirrels in the absence of predation. Ground squirrels competitively exclude snowshoe hares because their use of herbs is more efficient. Once snowshoe hares are excluded, (a) shrubs recover back toward their maximum biomass and herbs reach equilibrium with ground squirrels, and (b) snowshoe hare and ground squirrel recruitment efficiencies are set to 3 and 6.6, respectively.

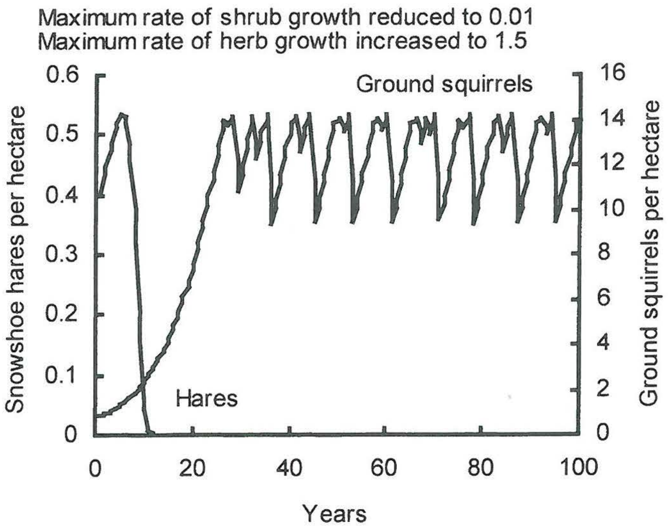

Figure 18.9 The effect of reducing the maximum rate of shrub growth and increasing the maximum rate of herb growth on competition between snowshoe hares and ground squirrels in the absence of predation. Ground squirrels competitively exclude snowshoe hares despite significantly higher productivity at the next trophic level down, vegetation.

snowshoe hare populations, forcing snowshoe hares to compete directly with ground squirrels for available herbs. Because ground squirrels have a more efficient functional response than snowshoe hares, the herb biomass that allows them to generate positive rates of increase is lower than that for snowshoe hares. Hence, herb offtake by ground squirrels reduces herb biomass to levels where snowshoe hares cannot sustain themselves in the modeled system. Even when the productivity of herbs is increased dramatically (maximum herb growth rate tripled to 1.5), competition from ground squirrels excludes hares from the modeled system (figure 18.9).

18.4.3 Adding Predation to Models of Interaction between Herbivores and Vegetation

We added estimated rates of offtake by predators (chapters 8 and 9) to the model of interaction of snowshoe hares and ground squirrels with their food resources. Estimated levels of predation could not be sustained by either snowshoe hares or ground squirrels at demographic efficiencies that produced equilibria between herbivores and their food resources. Increasing the demographic efficiencies of snowshoe hares and ground squirrels allowed them to sustain increasing levels of predation offtake. However, at most, 70% and 40% of estimated predation could be sustained by snowshoe hares over winter and summer, respectively, and 60% of estimated predation could be sustained by ground squirrels over summer. This suggests that either the estimates of predation obtained overstated actual predation rates, or the productivity of the vegetation–herbivore model was too low at some basic level. Productivity of the vegetation–herbivore model is largely determined by vegetation growth rates and maximum herbivore recruitment. Productivity levels for shrubs and maximum recruitment rates for snowshoe hares and ground squirrels were well documented. However, few data were available with which to estimate rates of growth in summer vegetation. Similarly, potential effects of resource-dependent dispersal or habitat use were not included in the model despite both being postulated as important factors linking predation, food availability, and herbivore demography (chapters 8 and 9).

Notwithstanding the limited capacity of the vegetation–herbivore model to sustain observed rates of predation offtake, the general patterns of variation predicted for snowshoe hares and ground squirrels appear plausible. For example, increasing recruitment efficiency for snowshoe hares to a value of 9 and adult survival efficiency to 1.7 produced a cycle in snowshoe hare abundance that mirrors that on control sites (figure 18.10). Similarly, increasing both recruitment and adult survival efficiencies for ground squirrels to a value of 12 allowed them to persist through regular cyclic declines, albeit at a lower density than observed (figure 18.11).

Increasing the demographic efficiency of herbivores reduces the level of food intake they require to generate positive rates of increase. This, in effect, reduces the influence that variation in food availability has on demographic rates. However, in reducing the influence food has on herbivore demography, increased demographic efficiency negates the potential for stable interaction between herbivores and vegetation. For example, if predation offtake is removed from the model that produced regular cycles in snowshoe hare

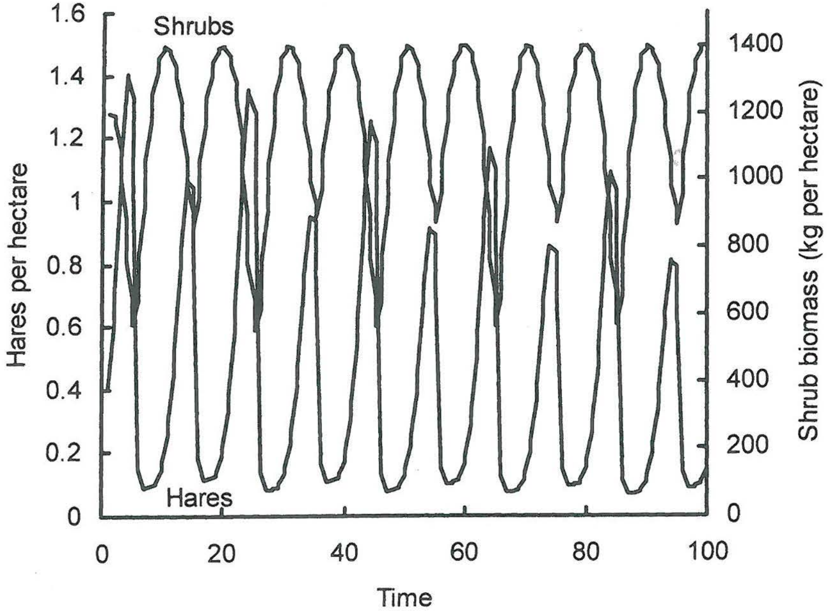

Figure 18.10 Reciprocal variation in the abundance of snowshoe hares and shrubs with 70% of observed predation rates over winter and 40% of predation rates over summer imposed on the model of interaction between herbivores and vegetation. Snowshoe hare recruitment efficiency is set to 9 and adult survival efficiency to 1.7.

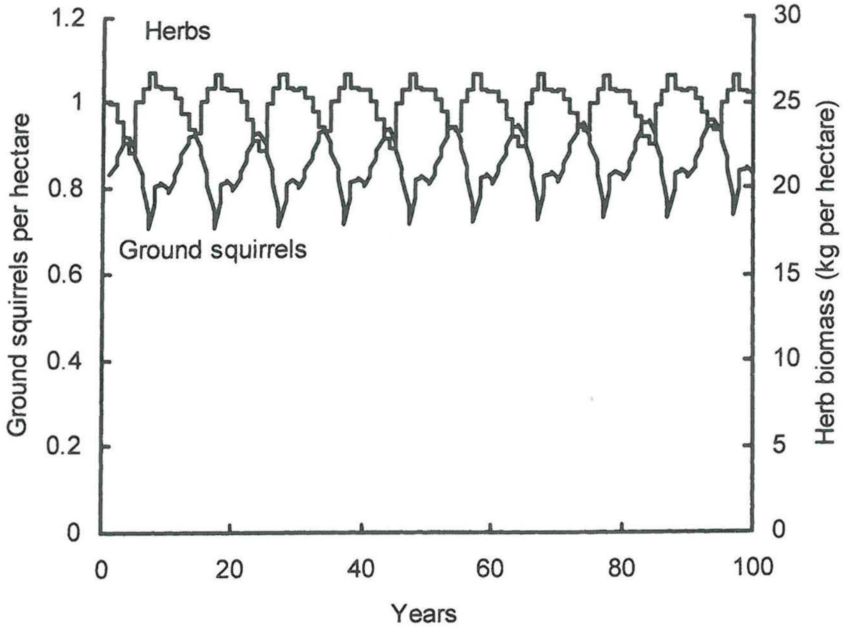

Figure 18.11 Reciprocal variation in the abundance of ground squirrels and herbs with 60% of observed predation rates over summer imposed on ground squirrels. Ground squirrel recruitment efficiency and adult survival efficiency are both set to 12.

abundance (figure 18.10), snowshoe hares erupt to densities where they decimate their food resources before crashing to extinction. This suggests that the demographic efficiencies necessary to sustain the high levels of predation to which snowshoe hares are typically exposed are incompatible with any sort of stable interaction between snowshoe hares and their food resources. This may not be surprising considering that the life history of snowshoe hares has evolved under continuous pressure from predators rather than absolute food shortage and that of the plants they exploit have evolved under conditions where excessive herbivory is apparently rare. Under these conditions, top-down processes would be expected to be more influential on community structure than would bottom-up processes.

18.4.4 The Effect of Herbivore Cycles on Predators

The model that linked observed changes in snowshoe hare and ground squirrel density to the three numerically dominant predators (lynx, coyote, and great horned owls) used the functional and demographic responses of each predator to variation in prey abundance (figure 18.12). We modeled functional responses using the same multiple-prey disc equation used to predict snowshoe hare diet (equations 2, 3; see worksheet "Predator functional responses" of Community.xls on the CD-ROM for additional details and parameter estimates). We used ground squirrels as a surrogate for all non-snowshoe hare prey exploited by these predators. Maximum intake rates and rates of effective search for snowshoe hares

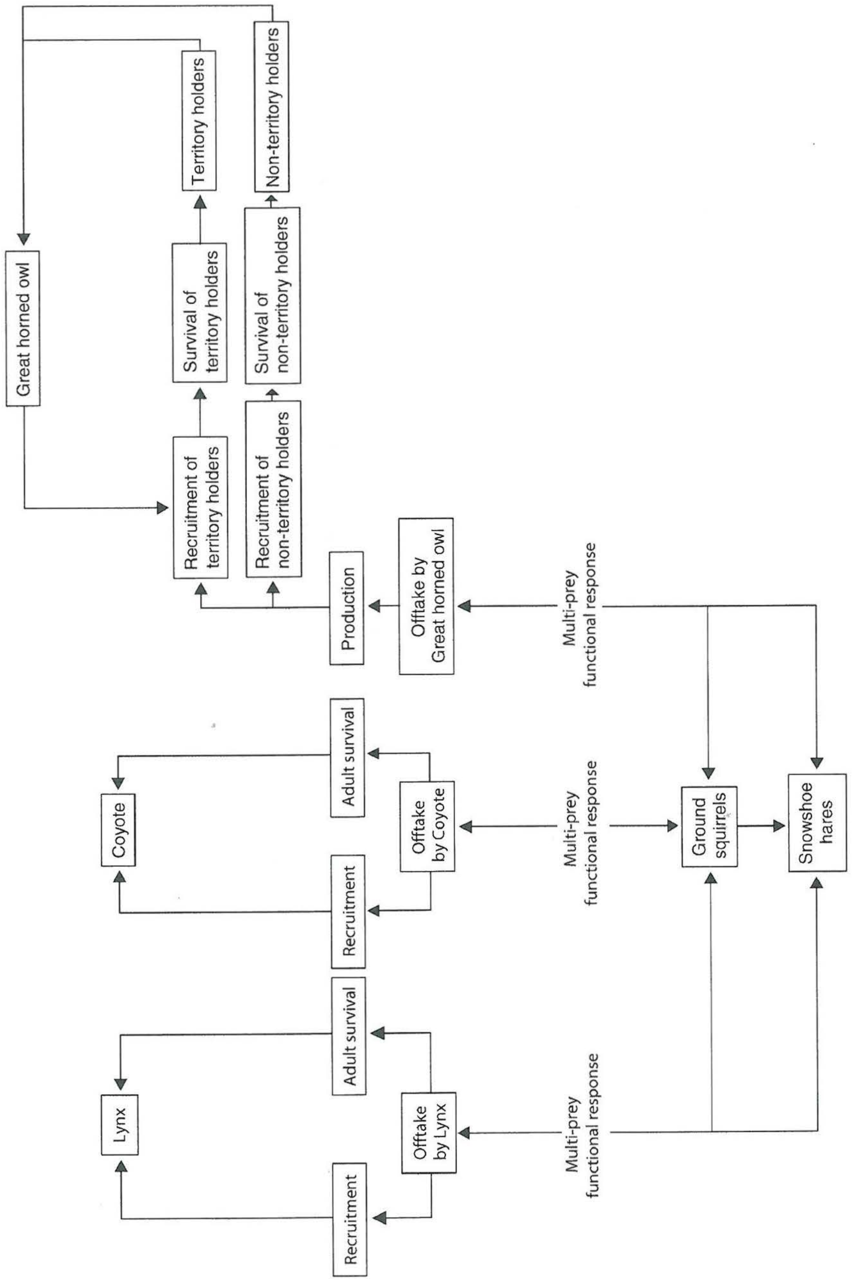

Figure 18.12 The structure of the model linking variation in snowshoe hare and ground squirrel density to the dynamics of lynx, coyote, and great horned owl populations.

were taken from chapter 13 for lynx and coyote and from chapter 15 for great horned owl. We estimated maximum intake rates for ground squirrels by assuming that 15% (by occurrence) of the saturated intake rate of each predator over summer was taken as ground squirrels (see chapters 13 and 15), that 90% of each ground squirrel was consumed, and that ground squirrels averaged 500 g body weight. Rates of effective search for ground squirrels were given values substantially less than those estimated for snowshoe hares to imply that snowshoe hares, when available, were strongly preferred by all predators.

We simulated predator demography by linking variation in per capita recruitment and adult survival to average food intake over each 6-month period, using estimates of food deficit and the same general exponential saturation function used to simulate the dynamics of snowshoe hare and ground squirrel populations. The exponential function used to link recruitment (R) to food intake deficit (FD) was modified to the form:

$$R = R_{\max}[1 - e^{-(FD-FD_{min})d}], \qquad (5)$$

where $R_{\max}$ is maximum per capita recruitment, d is a measure of demographic efficiency describing the relative effect a decline in food intake has on recruitment, and $FD_{\min}$ is the minimum food intake deficit for any reproductive activity to occur. Addition of a minimum food intake deficit allows the apparent threshold in food intake necessary for predator reproduction to be simulated. Recruitment and adult survival over each sequential 6-month period of summer and winter were combined in an additive model predicting instantaneous rate of change (r) for lynx and coyote density. Because the great horned owl population was separated into territory holders and nonterritory holders, a more complex population model was developed. Only territory holders bred, with offspring recruited into either the territory holder or non–territory-holder subpopulations depending on the ratio of prevailing territory holder density to maximum territory holder density (the maximum observed density of territory holders reported in chapter 15). The two subpopulations were subject to different rates of adult survival, with nonterritory holders having higher maximum density but a minimum food deficit below which survival fell to 0.

Predator population models were fitted by varying their component demographic efficiencies until good visual agreement between predicted and observed densities was obtained. In all cases, the demographic efficiencies of population models could be varied to predict predator densities that corresponded closely with estimated densities (figure 18.13). To evaluate the effect that the duration of the low-phase in prey abundance had on the degree of competition between predators, we added four 6-month periods (2 years) to the cycle of observed snowshoe hare and ground squirrel densities, at the point where snowshoe densities reached their minimum observed level (i.e., 0.065 hares/ha in spring 1994). Extending the low-phase of prey abundance resulted in the extinction of lynx and coyote over five protracted cycles and slightly reduced peak densities of non–territory-holding great horned owls (figure 18.14). This outcome is consistent with competition between predators intensifying as the period over which prey are in short supply is extended.

The effect that duration of the low phase in cyclic prey populations has on the potential for coexistence among predators is a specific example of a nonequilibrium outcome for a normal competition model (Tilman 1982). The fact that great horned owls are able to tolerate increases in the duration of the low phase in cyclic prey abundance clearly indicates that they are competitively superior to lynx and coyote. It follows that lynx and coyote are only able to coexist in the normally cycling system because they have a greater

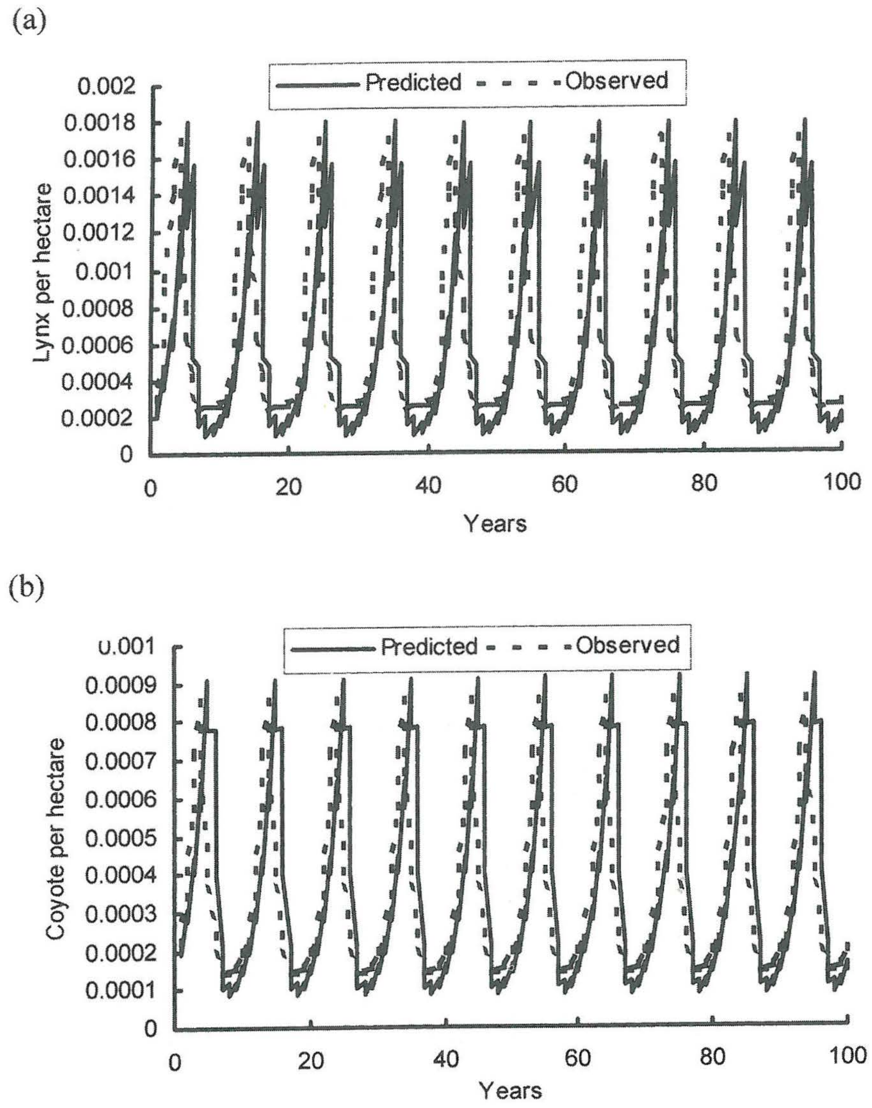

Figure 18.13 Predicted and observed variation in densities of (a) lynx, (b) coyote, and (c) predicted and (d) observed variation in the density of territory holding and non–territory-holding great horned owls.

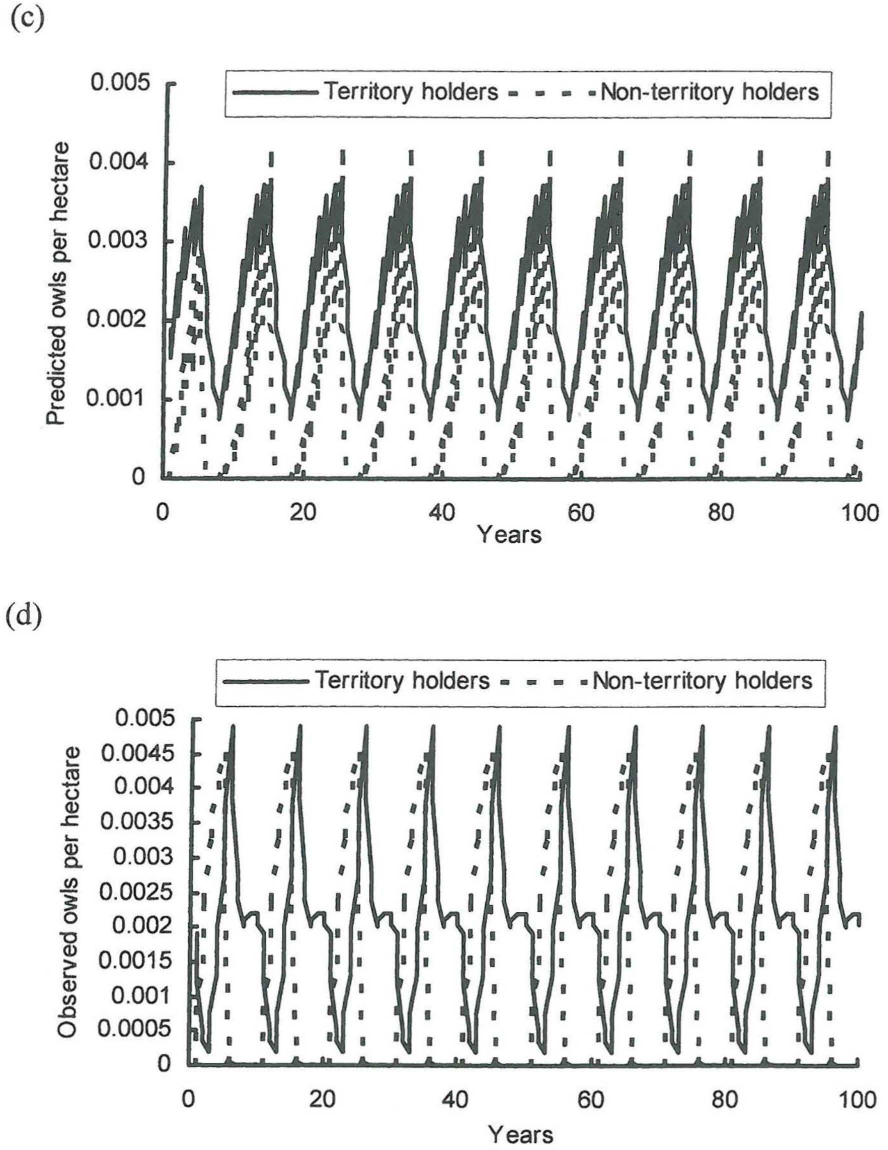

Figure 18.13 *continued*

capacity for increase than do great horned owls when prey are not limiting. The competitive superiority of great horned owls reflects the ability of reproductively active individuals (territory holders) to monopolize resources throughout the prey cycle and their conservative reproductive strategy relative to their mammalian counterparts during the cyclic low in prey availability (chapter 15). Extending the low-phase in cyclic prey abundance to 6 years results in great horned owl extinction over seven protracted cycles, indicating that even these tactics have their limitations.

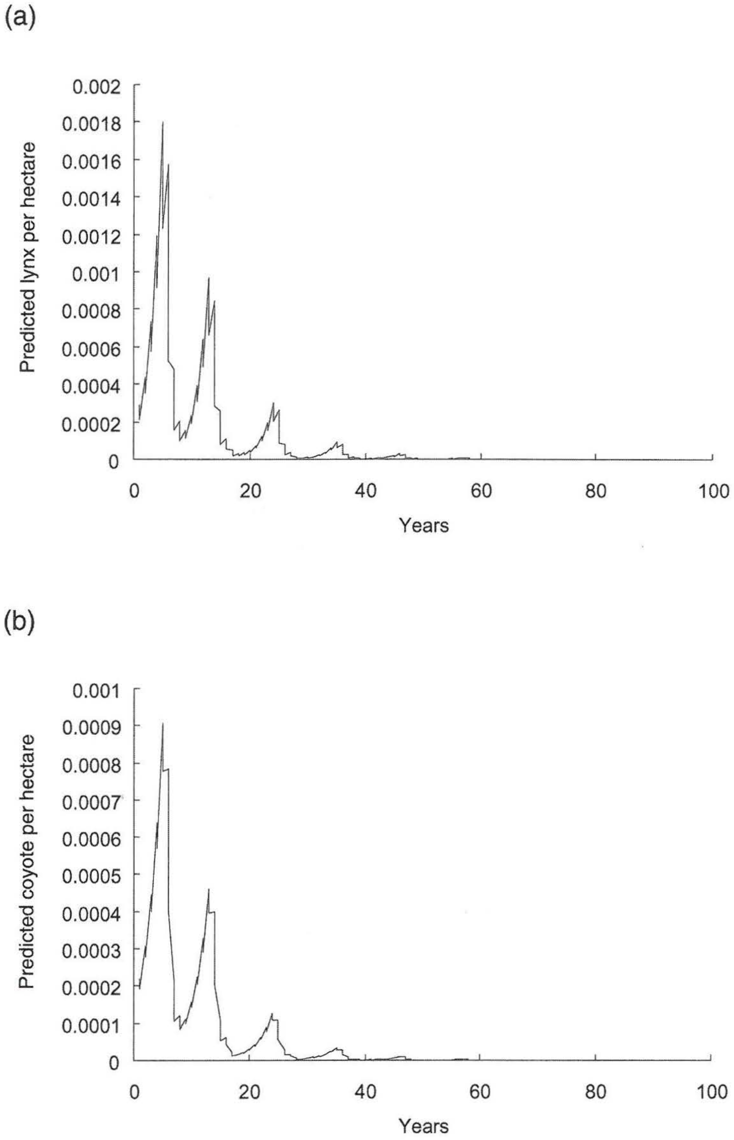

Figure 18.14 The effect on predators of adding 2 years to the low-phase of snowshoe hare and ground squirrel population cycles.

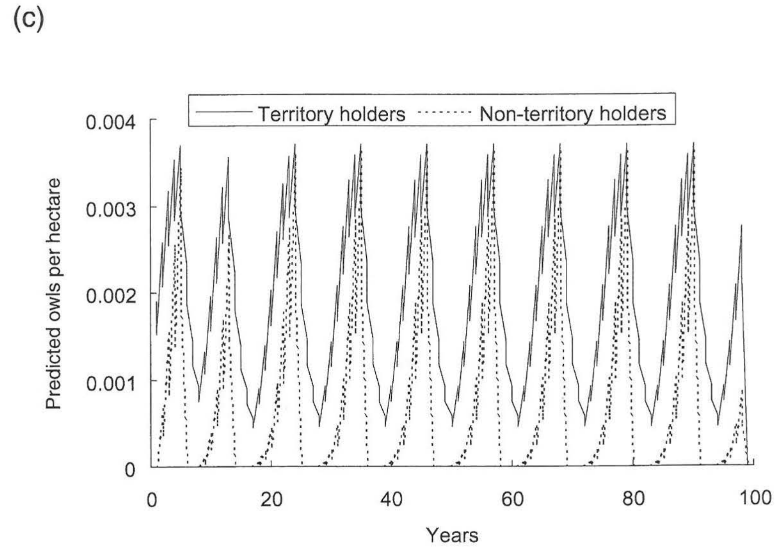

Figure 18.14 *continued*

18.5 Discussion

18.5.1 Unresolved Modeling Issues

The models described in this chapter explored the effect observed rates of predation had on predicted interaction among snowshoe hares, ground squirrels, and their food resources and the effect that observed variation in snowshoe hare and ground squirrel density had on predicted variation in the abundance of their predators. To link the dynamics of predators and prey in a full simulation of interaction among vegetation, herbivores, and predators, observed rates of predation and observed variation in prey abundance would have to be replaced with their predicted counterparts. Despite considering a complete range of demographic efficiencies for both herbivores and carnivores, we were unable to identify parameter values that allowed this replacement while maintaining stable outcomes for predators, prey, and vegetation. This suggests that either parameter values used in other parts of the model are inaccurate or that some important stabilizing mechanisms are missing from the model.

Many parameters used in the model had to be guessed (e.g., rates of effective search for predators consuming ground squirrels), derived indirectly (e.g., demographic efficiencies for all species), or modified from their original values (e.g., predation rates on snowshoe hares and ground squirrels). Hence, although the model is structurally accurate, it is likely that many of the parameter values it uses are not. Similarly, although the model includes the important trophic interactions that influence the structure of the modeled species (i.e., functional and demographic responses), other mechanisms that may enhance community stability by modifying these interactions have been omitted. In particular, the suite of prey species exploited by predators as an alternative to snowshoe hares have been replaced with ground squirrels as a surrogate. Likewise, the tendency for predators to prey upon each other when snowshoe hare and ground squirrel abundance was low has been ignored. Both of these mechanisms would tend to stabilize the interaction between predators and their primary prey by modifying the efficiency of functional and demographic responses at critical phases of the cycle in predator density.

Another potentially important omission in the models described here is the lack of spatial behavior by predators or prey. Large-scale dispersal patterns can to some extent be encompassed by the demographic rates of the species they effect, but smaller scale shifts in habitat preference cannot. These sorts of behaviors may be important influences on the susceptibility of prey to predators and on the efficiency with which predators and prey can use available food resources. Hence, by not explicitly or implicitly representing these effects, the models described may be ignoring important sources of stability in the dynamics of vertebrates in this ecosystem.

It may be feasible to build all or any of this additional complexity into the existing models, but this would require estimates of a whole suite of additional parameters for which few data are available. For example, if predation efficiency is influenced by habitat, the disc equations used in the models described here would need to be modified so that changes in habitat use associated with different phases of the snowshoe hare cycle could be represented. This would be a complex undertaking (particularly for the multispecies equations used for snowshoe hare foraging and for predators) that would be made more difficult when any influence of habitat on predation efficiency varied between prey species. However, regardless of how complex such an undertaking may be, it would be essential if habitat-related constraints on predation efficiency was an important influence on community structure and stability in the boreal forest. This suggests that the view that simple models of interaction between a population and its food resources can be "piled-up" to consider more complex questions about communities may be naïve (Pimm 1991). Where indirect processes such as those related to habitat effects are an important influence on community structure and function, more complex mechanistic models would need to be developed. The data required to parameterize and validate such models will be difficult and expensive to acquire, and the mathematical framework within which to use these parameters will be difficult. For example, the sensitivity of the simple models described here to small shifts in parameter values reflects the relatively coarse time-step we have used (6 months). However, although a continuous-time modeling approach would provide more stability, complex mathematical approaches would be needed to adapt this approach to the seasonal nature of the modeled ecosystem (e.g., La Place transformations; Renshaw 1991). For most real communities, the mathematical complexity required to accommodate the full range of biotic and abiotic processes that influence structure and function rapidly outstrips the capacity of biologists to supply sufficient data. This does not mean that modeling cannot contribute greatly to our understanding of community dynamics, but rather that modeling should focus on the mechanisms that influence the structure of community components, not on the structure of the community as a whole. In essence, this is what most mechanistic models of biological communities have attempted (Tilman 1982).

18.5.2 Mechanisms of Coexistence

Although the analysis of stability for co-occurring snowshoe hares and ground squirrels suggested that their food resources were sufficiently different that they could coexist, the demographic efficiencies used in these models were substantially lower than required to sustain observed levels of predation. When demographic efficiencies were increased to levels where snowshoe hares and ground squirrels could cope with observed levels of predation, their interaction with food resources became unstable. Hence, in the absence of predators, it seems probable that snowshoe hares and ground squirrels would compete fiercely for available food resources and that one species could exclude the other. Under these circumstances, the coexistence of snowshoe hares and ground squirrels would be mediated by predation. Predator-mediated coexistence is considered a widespread phenomenon among phytophagous insects, but it has been less commonly demonstrated among herbivorous mammals (Lawton and MacGarvin 1986). However, recent analysis of predator–prey and vegetation–herbivore interactions in several mammalian communities suggests that predation is important for facilitating the coexistence of at least some mammalian herbivores (Moen et al. 1993, McLaren and Peterson 1994, Sinclair 1995).

The way in which trophic interaction influences competition and coexistence among the three modeled predators is more straightforward. All three predators are extremely reliant on snowshoe hares; none is able to generate positive rates of increase when snowshoe hare abundance is low. The important difference between these predators is the rate at which they decline during the low phase of cyclic snowshoe hare density and the rate at which they increase when snowshoe hare density recovers. The results of the modeling summarized here suggest that great horned owls have the lowest rates of decline over the low phase, but also the lowest rate of increase after snowshoe hare density recovers. This places great horned owls at a competitive advantage over lynx and coyote during the low phase but at a disadvantage over the period of high snowshoe hare availability. The net result of this trade-off is that, although great horned owls will have the same reciprocal cycle in density as lynx or coyote, their cycles will tend to be of lower amplitude. This places them at less risk of localized stochastic effects that may affect their density or that of their principle prey directly. As such, great horned owls may be less reliant than lynx or coyote on dispersal as a means of maintaining their populations throughout the boreal forest.

18.5.3 Top-down and Bottom-up Influences on Community Structure

The analyses described in chapter 17 did not specifically consider the complexity that nonlinear interactions between trophic levels would introduce to models describing the influence that different trophic levels exert over each other in the boreal forest (i.e., the saturating functional and demographic responses used in the models described here). However, it was argued that these complications would not alter the qualitative conclusions drawn from the simple linear models of interaction used in those analyses. Collectively, the modeling results for herbivores and their interaction with food resources and predators described in this chapter support the reciprocal effects model advocated in chapter 17. Although predation clearly dominates changes in the biomass of herbivores in the boreal forest, food limitation has an important if less dramatic influence on the dynamics of snowshoe hares and ground squirrels.

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