

Theoretical Insights into the Population Viability of Lynx

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Abstract—We discuss ecological theory and population models pertinent to the population biology of southern lynx. Fragmented forest cover types, high vagility of lynx, and linkages in population dynamics suggest that lynx in the contiguous United States are arranged as metapopulations. Metapopulation stability depends on not only habitat quality but also dispersal rates between habitat islands. Models indicate that dispersal rates between habitat islands should sharply decrease as the islands become smaller and more distant and the risks associated with crossing between islands increase. Southern lynx populations may fluctuate, which affects both rates of extinction and colonization of habitat islands. Synchronous population fluctuations can decrease the viability of metapopulations. Southern habitat islands probably are source-sink mosaics that shift with disturbance and succession. Models indicate that temporally transient habitat may be underutilized by organisms. Lagged synchronous patterns observed in both northern and southern populations suggest broad connectivity between subpopulations, but empirical

data are lacking and some subpopulations may be isolated. Models that combine dispersal into spatial predator-prey models generate similar patterns, and dispersal can provide a synchronizing mechanism. We emphasize the dangers associated with ignoring either local habitat quality or regional connectivity.

Introduction

To conserve lynx we must rely on both applicable ecological theory and specific information about lynx ecology like that presented in the middle section of this book. The purpose of this chapter is to review the ecological concepts and parameters used in evaluating population viability. We identify some of the specific problems associated with applying these concepts to lynx.

Population Viability

The population, not the species, is the appropriate taxonomic level of focus for most conservation efforts (Chapter 5, Ruggiero et al. 1994). The National Forest Management Act of 1976 requires the U.S. Forest Service to maintain viable populations of all native vertebrate species, and the Endangered Species Act of 1973 recognizes distinct population segments as appropriate levels of statutory protection. Biologically, the importance of maintaining viable populations is based on the idea of ecological dependency (Ruggiero et al. 1988), which implies a dynamic relationship between a population and the environment that supports it.

Population viability refers to the probability that a population will persist for a specified time into the future (Boyce 1992). Formal Population Viability Analysis (PVA), however, requires information on many variables that are difficult to estimate for low-density populations (Beissinger and Westphal 1998) like the lynx. For even the simplest deterministic models, information on age structure, breeding schedule, and survival rates are needed. These models assume that demographic rates are constant, which certainly is not true for lynx. Given even this minimal list of parameters, we cannot build these models for southern populations of lynx given the scarcity and uncertainty of data on lynx vital rates (Chapter 13). We can, however, evaluate ecological theory as it pertains to lynx at the southern periphery of their range and evaluate potential risks to population persistence.

Stochastic Factors That Affect Viability

Small populations are usually thought to have low viability because of their vulnerability to chance events. The elements of chance that affect viability are demographic stochasticity, environmental stochasticity, genetic stochasticity, and catastrophe (Shaffer 1981). Demographic and environmental stochasticity are terms generally associated with birth and death rates. Demographic stochasticity refers to chance events that work at the level of the individual; environmental stochasticity to chance events that affect the vital rates of the population such as low reproductive rates during a drought.

Catastrophes differ substantially from either demographic or environmental stochasticity. Both demographic and environmental stochasticity affect expected times to extinction and are sensitive to population size. Catastrophes can eliminate an entire population at a single moment in time regardless of its size. Many catastrophes are associated with disturbance processes such as fire, flood, or volcanic eruption and have limited geographic scope. Such processes may kill all of the organisms within the disturbed area, but populations outside will be unaffected. In species like the lynx with a broad geographic distribution, catastrophe is not likely to play a major role in species persistence. However, small southern populations of lynx could be affected by catastrophic events, with consequences for viability in the contiguous United States.

Genetic stochasticity is similar to demographic stochasticity but operates at the genetic level and is expressed indirectly through demographic processes (Saccheri et al. 1998). For example, genes associated with disease-resistance may be lost by chance in matings among closely related individuals, and the resulting progeny would experience increased mortality rates. In small populations, this can produce a positive feedback between genetic and demographic processes: genetic losses reduce fitness, which leads to smaller populations, increased rates of genetic loss, and further fitness reductions. This process has been called an extinction vortex (Gilpin and Soulé 1986).

The genetic properties of populations are vital to both short and long term population persistence and these issues are discussed more fully in Chapter 5. In this chapter, the models and theory deal strictly with demographic processes and do not address the genetic processes described above. While ignoring genetic factors is clearly artificial, genetic and demographic processes tend to happen at very different rates. For instance, demographic population rescue requires that enough immigrants enter a population on average to make up the difference between population losses (emigration

and mortality) and birth rates. This rate of immigration is generally several orders of magnitude greater than is necessary to accomplish genetic rescue, which entails offsetting the loss of alleles through genetic drift (See Gilpin 1991 for a discussion of genetic drift in small, fragmented populations).

Population Viability Concerns for Southern Lynx Populations

Southern lynx occur at relatively low densities, are found almost exclusively in cool, moist, coniferous forest types (Chapter 8), eat a winter diet dominated by two species (snowshoe hare and red squirrel; Chapters 9 and 13), and, at least in Canada and Alaska, exhibit strongly cyclic population dynamics (Chapter 9). In the contiguous United States, forest cover types in which lynx have occurred are either peninsular extensions of larger habitat areas in Canada or discrete islands (Chapter 8, Figs. 8.19-8.23, Map Insert). Given the low densities of lynx in these southern habitats (Chapter 13), many of these habitat islands will contain relatively few individuals and may collectively function as metapopulations. Alternatively, many of these habitat islands may function as separate, isolated populations unto themselves, rendering each isolated population highly vulnerable to extirpation.

In southern boreal forests, hares appear to exist in many areas at densities close to the lower limits required for lynx reproduction (Chapter 7) and lynx densities are correspondingly low (Chapter 13). Prey densities vary with forest type and stand age. For a population at equilibrium (birth rates = death rates), small changes in habitat quality can produce a sink (birth rates < death rates). Because southern lynx populations appear to exist close to this threshold, southern lynx habitat probably is a shifting mosaic of source and sink areas.

Lynx populations in the taiga exhibit cyclic dynamics with high-amplitude fluctuations (Elton and Nicholson 1942; Stenseth et al. 1997; Chapters 8, 9). There is some evidence that hares (Chapter 7) and lynx (Chapter 8) fluctuate in the south as well. Population fluctuations potentially change the dynamics of local extinction and colonization, and can produce a number of unique spatio-temporal patterns such as travelling waves (Okubo 1980). These are population fluctuations that move, like waves, across broad geographic areas (See Moss et al. in press for a well-documented example). Adjacent geographic areas experience peaks and troughs that are lagged behind those at the origin of the wave, producing the “lagged synchrony” referred to in later chapters.

Based on these understandings, we believe that three areas of ecological theory are particularly pertinent to southern lynx populations: metapopulation dynamics, source-sink habitat relationships, and special properties of cyclic systems.

Metapopulation Dynamics

Metapopulation models view a population as a number of discrete subpopulations within habitat patches or “islands” connected by dispersal. Through time, subpopulations may go extinct and be recolonized, but the larger metapopulation persists. The original metapopulation model described a population of equal-sized habitat islands separated by areas that contained no resident organisms, but which allowed dispersal (Levins 1969, 1970). According to the model, subpopulations were in one of two states: either populated or extinct. The dynamics of Levins’ model are described by the differential equation:

$$\frac{dp}{dt} = mp(1 - p) - ep \quad (1)$$

where p is the proportion of habitat islands occupied, m is the colonization rate, and e is the extinction rate of the subpopulations. The expected equilibrium proportion of occupied islands is:

$$\hat{p} = 1 - \frac{e}{m} \quad (2)$$

Hence, if the extinction rate is less than the colonization rate, the metapopulation will persist on at least some of the islands. If the subpopulations are completely isolated, ($m = 0$), then the metapopulation cannot persist.

An important inference from this model is that when the rate of local extinction equals that of colonization, all islands are unoccupied and the entire metapopulation goes extinct. For most of the islands in a metapopulation to be occupied at a given time, the colonization rate must greatly exceed that of local extinction. If subpopulations on islands are extinction-prone, then a stable metapopulation requires a high rate of dispersal between the islands.

Recently it has been argued that classical metapopulations, consisting of equal-sized, equidistant islands, are a theoretical construct that rarely exists in nature; mainland-island systems in which one island is much larger than the others are more common (Hanski 1982; Harrison 1993). These systems are not prone to the same kinds of instabilities as classical metapopulations, because the mainland is large enough that its population is not prone to extinction. However, Harrison’s (1993) criticism of applying metapopulation theory to conservation is pertinent only if one is concerned just with the persistence of the mainland population. For lynx in the contiguous United States, we are interested in the dynamics of the islands, where population persistence will be determined by colonization and extinction rates among habitat islands.

Colonization

The effect of distance—Assuming a habitat island is unoccupied, its colonization will occur through the dispersal of organisms from either other islands or the mainland. The probability of colonization will be a function of the number of dispersers, and the distance to and difficulty of reaching the islands. Lamberson et al. (1994) modeled dispersal between same-sized habitat islands by partitioning the probability into two components: the time it takes to travel to the island (and hence the probability that the organism will live long enough to reach it), and the likelihood that a dispersing individual will encounter the island. For an organism to successfully disperse, it needs to survive long enough to reach the island and it needs to travel in the right direction. Thus, the probability of successful dispersal rapidly declines with distance. For a single distant island, only a small proportion of dispersers will travel in the right direction and, if dispersal is risky, many will die in transit. We illustrate this using the algorithms presented by Lamberson et al. (1994). If an organism travels in a straight-line 1 km per day and has a 1% chance of mortality per day while dispersing, 13.5% of the dispersers will find a 10-km wide island at a distance of 10 km. Only 0.7% would find that same island at a distance of 100 km. This estimate of the decline in probability of successful colonization with distance probably is conservative. Lamberson et al. (1994) assumed a constant probability of mortality for each time-unit spent dispersing, but it is likely that death rates increase as dispersals get longer. During dispersal, organisms are thought not to forage as efficiently as in a home range, and the disperser's body condition likely will decline with time. Thus, dispersal across long distances is risky, and successful colonization will be rare. If a disperser stops at the first suitable site, this behavior leads to a geometric decline in dispersals with distance, a pattern observed in a variety of organisms (Waser 1985; Buechner 1987).

Dispersal in spatially heterogeneous, cyclic populations—Levins' (1969,1970) metapopulation model assumes equal habitat conditions in all islands and constant rates of dispersal over time. *Lynx*, at least in the taiga, display strongly cyclic population dynamics. In non-cyclic populations, dispersal is thought to be a relatively passive process; a proportion of the population disperses, and that proportion is determined by the evolutionary consequences to fitness of dispersing and its opposite, philopatry (Hamilton and May 1977). In temporally stable habitats, dispersal should generally lead to decreased fitness and therefore should not be favored (Hastings 1983; Holt 1985). In a temporally unstable environment, however, dispersal can be favored even if fitness costs are high (Levin et al. 1984; Frank 1986; Cohen and Levin 1991).

Dispersal may be particularly important for regulating cyclic populations, but the mechanisms are poorly understood. Krebs (1992) described a phenomenon, the “fence effect,” in voles: if a vole population is physically enclosed (“fenced”), the population will rise to high densities and subsequently crash, a dynamic not seen in adjacent unfenced populations. Here, dispersal is a pre-saturation phenomenon with a population-regulatory function. Krebs (1992) speculated that cyclic populations are characterized by pre-saturation dispersal, whereas non-cyclic populations exhibit saturation dispersal. In general, dispersal is thought to be more critical for cyclic populations and may help generate or propagate the cycles. In Canada, lynx are strongly cyclic, but long-range movements are more frequent during those periods when hares are rapidly declining (Chapter 9), indicating post-saturation dispersal. The extent to which these movements result in successful dispersal is, however, unknown.

Successful dispersal—Colonization of islands in a metapopulation differs fundamentally from within-island or within-mainland dispersal, in that the latter does not require crossing extensive unsuitable habitats. Dispersal, by definition, describes movement from site of origin to site of next mating, and successful dispersal to the entire process of movement, subsequent mating, and production of young (Shields 1987). If dispersal to distant habitat islands is rare, successful dispersal must be even more so. Early models (e.g. MacArthur and Wilson 1967; Richter-Dyn and Goel 1972), concerned only females, and males were assumed to either automatically follow along or to have impregnated females before dispersal. For most mammals that do not exhibit embryonic diapause, these assumptions are unrealistic; successful dispersal requires, at the very least, a male and a female to arrive at the destination at about the same time. In the example above, if the source island produced 10 dispersers per year, then about one animal per year would successfully disperse 10 km. If the organism were fairly long-lived, this would provide a reasonable probability of a mating pair co-occurring in the destination island and dispersing successfully. At 100 km, however, a dispersing animal would find the island only once every 14 years, greatly reducing the probability of successful dispersal.

These problems are exacerbated if long-range dispersal is sex-biased. It is widely believed, for example, that dispersal in many mammals is male-dominated (Greenwood 1980; Cockburn et al. 1985; Clark et al. 1988), although for many species the evidence is weak (see Gaines and McClenaghan 1980) and based on questionable methods (Porter and Dueser 1989). Still, if most long-range dispersal were by males, then simultaneous male-female occurrences at destinations would be rarer than overall dispersal rates suggest. Data on lynx in southern Yukon concerning sex-bias in emigration

are equivocal. In general, rates of emigration showed no sex bias, but 14 of 17 detected movements >100 km were males (Chapter 9). Data on rates of dispersal, successful and otherwise, are few. Dickman and Doncaster (1989) found that in urban environments wood mice and bank voles recolonized distant sites (200-400 m) more slowly than close sites (50-140 m).

The previous discussions concerning dispersal only consider animals that move independently and disperse in random directions. These assumptions may be inappropriate. Animals may have knowledge acquired through exploratory movements or may have direct visual clues that allow them to move directly from one habitat island to the next. Similarly, if an organism leaves a scent trail during dispersal, then other dispersers can follow it thereby increasing the number of dispersers that reach a specific location. We do not know if lynx have dispersal mechanisms that allow them to more efficiently colonize islands, but exploratory movements appear to be fairly common in southern populations (Chapters 11, 13).

Introductions and reintroductions of organisms, which are human-facilitated dispersals, are better documented than natural dispersal events. Introductions allow us to look at the likelihood of success, given dispersal. Although introductions and dispersal differ in important ways, some of the factors that lead to failure (animals arriving in poor condition, behaviors poorly adapted to the destination, importance of stochasticity in small populations) will be similar. Importantly, introductions are intended to succeed and designed to that end. Even so, introductions often fail. In desert bighorn sheep, all introductions in which the initial population was less than 50 individuals failed within 50 years (Berger 1990). Of 353 insect introductions to control exotic weeds, 70% failed, and success was insensitive to initial population size: 66% of the introductions in which the initial population was ≤ 20 failed compared with 70% of those with initial populations >100 (Simberloff 1989). It is reasonable to conclude that even with large numbers of dispersers, colonization will frequently be unsuccessful.

Pulsed dispersal and colonization—The role of cyclic dispersal in colonization has been little studied. As we have shown, colonization of distant areas is very unlikely if animals disperse at constant rates over time. If, however, dispersers are pulsed so that at some times many dispersers are searching simultaneously, then the probability of distant colonization increases significantly. Assume, as in our earlier example, that each disperser has a 0.07% chance of successful arrival at a habitat island, that 90% of those that arrive survive for a year, and that at least two animals co-occurring at the destination will result in colonization. If the source population produces 10 dispersers every year then, on average, the island will have ≥ 2 organisms about 3% of the time. If, however, 100 dispersers are

produced once every 10 years, this increases to about 10%. Of course, not all sets of two organisms will mate; they will be of the same sex about half the time. If we assume that at least four organisms are needed for colonization, producing 10 dispersers per year will virtually never achieve this (0.05%), whereas a 10-year pulse of immigrants will put ≥ 4 organisms on the island about 8% of the time.

Extinction after successful dispersal—After a habitat island is colonized by successful dispersal, the risk of extinction should decrease as the population gets larger. But the relation between extinction risk and population size is critically dependent on the kind of extinction risk. Early models (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972) considered only demographic stochasticity. Demographic stochasticity in a very small population can be viewed as being similar to a series of coin flips: if heads the population decreases by one, if tails, it increases by one. If population size = 3, then HHH would cause extinction, as would HHTHH. In very small populations, random events leading to extinction are likely and extinction rates are high. As population size increases, even to as few as 20 reproducing females, the probability of this type of random event leading to extinction becomes vanishingly small (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972).

If demographic stochasticity were the only extinction risk, then except for tiny, isolated populations metapopulation dynamics would be unimportant. However, environmental stochasticity, including weather, affects the demography of the metapopulation. Harrison and Quinn (1989) included correlated environmental stochasticity in a model of metapopulation dynamics and found that if the means and variances of subpopulation extinction rates were high, temporal correlation of subpopulation events greatly reduced the average time to metapopulation extinction. However, if the extinction rate of subpopulations was low or moderate and consistent among subpopulations, high environmental correlation among subpopulations did not predispose the metapopulation to go extinct. The largest differences between correlated and non-correlated systems were seen in metapopulations with many islands. So, number of islands in a metapopulation, rate of subpopulation extinction, and environmental correlation among subpopulations are all related to the persistence of metapopulations.

Source-Sink Dynamics

Southern lynx populations appear to exist at lower densities and to have lower reproductive rates than northern populations (Chapter 13). Habitat

heterogeneity is also much higher than in the taiga (Chapter 3); therefore, southern populations likely occur partly in areas which act as “sinks” and are dependent on immigration from “sources.” Source environments produce surplus animals, which must disperse to have a chance of surviving. Sink environments do not produce enough animals to sustain themselves and, in the absence of immigration from source areas, populations living in sink areas go extinct (Pulliam 1988). To determine whether a particular area is a source or a sink, we need to know the birth and death rates of the population (Krebs 1994). We cannot use the surrogate measure of population density to determine source or sink environments; ecologists have repeatedly pointed out that sink areas may contain high population densities (Van Horne 1983; Hobbs and Hanley 1990).

In source-sink models (Pulliam 1988; Pulliam and Danielson 1991; Howe et al. 1991) equilibrium dynamics depend on specific rules concerning habitat selection, as well as the vital rates associated with the source and sink areas. If, for instance, a few areas were very productive, but in the rest of the landscape birth and death rates were nearly in balance, a very large population could be supported by a few source areas. Conversely, the loss of a few important areas could destabilize a very large population that depended on sources to maintain population viability.

Source-sink dynamics tend to be modeled as spatial rather than temporal; a given area is assumed to be either a source or a sink environment permanently (Pulliam 1988; Pulliam and Danielson 1991). Source-sink concepts as they relate to lynx, however, are complicated by strong temporal components. In the North, the same areas that produce excess animals at one phase in the cycle are strong sinks a few years later. Similarly, because the densities of prey change as stands undergo succession (Chapters 6, 7, and 14), areas that are sinks today may be sources in a few decades, or vice-versa. When evaluating landscape-level changes and their impacts on source-sink dynamics, it is therefore necessary to determine both current and long-term productivity of a particular area.

Fahrig (1992) modeled habitat change using a simple model in which habitat was either suitable or not and found that the model was far more sensitive to turnover rates of habitat than it was to the distance between habitat islands. While not a source-sink model in a formal sense, it indicated that temporal changes in habitat quality could have a profound impact on population stability. To address this question using a source-sink model, Pulliam et al. (1991) built a more complex simulation model for the Bachman’s sparrow (BACHMAP; Pulliam et al. 1991) that allowed habitat areas to change quality over time so as to simulate active forest management. Bachman’s sparrow, which historically was found in old pine forests, has declined over much of its range (Pulliam et al. 1991). An interesting aspect

in this decline is that Bachman's sparrows breed in newly planted pine fields as well as old-growth areas, but seldom in intermediate-aged stands (Pulliam et al. 1991). Young stands areas are plentiful in the short-rotation southern pine plantations, and reproductive rates in these areas are no different from those in old forests (Haggerty 1988). Source-sink dynamics were therefore allowed to vary; the highest recruitment rates were in very old and very young forests. Surprisingly, Pulliam's (1991) model consistently showed that population sizes were maximized when the largest amount of old forest was retained. As with Fahrig's (1992) model, the rapid turnover of the source habitat after cutting precluded its effective utilization.

Cyclic and Spatial Dynamics: Synchronizing Elements and Traveling Waves

Predator-Prey Dynamics

In mathematical models, populations of specialist predators can exhibit stable, cyclic, or chaotic behavior. These dynamics reflect interactions between the predator and the prey; the predator affects prey densities and is, in turn, affected by the prey (May 1973; Hanski et al. 1993). The inclusion of generalist predators, which can switch prey, tends to dampen cyclic behavior and produce more stable systems (Hanski et al. 1991). Because of prey-switching behavior, predator populations tend to become decoupled from dynamics of a specific prey (Erlinge et al. 1991; Hanski et al. 1991). For instance, in northern Canada coyotes depend entirely on snowshoe hares (O'Donoghue 1997, Chapter 4), and their populations cycle much like those of lynx in response to hare densities. Because they are hare specialists, their addition to northern ecosystems in the early 20th century would not necessarily change the cyclic behavior of hares or other hare predators. However, in areas farther south where coyotes switch to ungulate prey when hares are scarce (Chapter 4), we would expect them to have a very different influence. This is consistent with the generally stronger appearance of cyclic dynamics in northern, less species-rich ecological systems. Similarly, microtine rodent populations in northern Scandinavia are more cyclic than those farther south, likely because there are more generalist predators in southern areas (Erlinge et al. 1991; Hanski et al. 1991).

Diffusion-Reaction Models

Simple predator-prey models assume homogeneity in vital rates and the interactions between predators to prey. These models therefore apply only

to small geographic areas. For larger areas, predator-prey dynamics are linked through movement. The inclusion of movement into population models generally changes their dynamics. In many cases, dispersal acts to stabilize (Doebeli 1995) or synchronize (Blasius et al. 1999) intrinsically unstable or chaotic systems. These dynamics have been conceptualized as diffusion-reaction models (Okubo 1980), in which the diffusion is movement and the reaction is predator-prey dynamics defined in space and time.

Diffusion-reaction models tend to generate traveling waves (Skellam 1951; Okubo 1980), that resemble the cyclic behavior of lynx populations over broad geographic areas (Blasius et al. 1999). For instance, in the simple case where a population originates at a particular point in space and time, population growth will spread outward from that point in the form of a wave. The wave travels at a rate defined by the intrinsic growth rate of the population and the rate of movement (Okubo 1980; Shigesada and Kawasaki 1997). Unless the predator population is zero behind the frontal wave, the system is characterized by a “wake” of smaller following waves, the magnitude, duration, and character of which depend on characteristics of the system being modeled (Gurney et al. 1998). The degree to which actual dispersal behavior is correctly modeled by diffusion is unknown for most species. Skellam (1951), however, demonstrated that dispersal of muskrats in Europe closely followed model expectations.

Large-scale synchrony can be achieved through the coupling of cyclic or chaotic systems through dispersal (Blasius et al. 1999). Of particular interest to lynx dynamics is “phase synchronization,” characterized by synchronization of periodicity but not of amplitude (Blasius et al. 1999). This pattern, which appears to describe lynx dynamics in Canada during the 20th century (Chapter 9 Fig. 9.4, Blasius et al. 1999), occurs at intermediate levels of diffusive coupling.

Discussion

If a landscape provides small habitat islands, then the system will only be stable if it functions as a metapopulation. Very small isolated populations are subject to a variety of risks and are prone to extinction. For a metapopulation to persist, rates of colonization must greatly exceed rates of extinction. Colonization rates, in turn, are driven by the number of colonizers produced by the islands and the probability of successful dispersal between islands. Because metapopulations depend both on population size within and dispersals between islands, they can easily be destabilized. If, for instance, adult mortality were increased so that populations on the islands were generally below carrying capacity, even if these populations appeared

stable, dispersal would be greatly reduced: there would be fewer potential dispersers and more of these would likely remain on their natal islands. Similarly, maintaining populations on the islands at carrying capacity, but reducing between-island dispersal, would also potentially destabilize the metapopulation.

For lynx, it is likely that rates of dispersal between both the large mainland population in the North and between other islands in the contiguous United States are highly variable. Lynx populations therefore may exist as several smaller but effectively isolated metapopulations. Arguably, the lynx in the northeastern United States are effectively isolated from the main Canadian populations by the St. Lawrence Seaway (Chapter 8) and from the Great Lake States by agricultural conversion and urban development. Similarly, boreal forests in Colorado and Utah are separated from the larger areas of boreal forest in Wyoming by at least 100 km (Chapter 8). If these areas have become effectively isolated, then they represent special areas of concern and, if they still contain native populations, these populations are particularly endangered.

We know very little about lynx biology in the southern portions of its range, but the population dynamics we observe are complex and appear to be spatially interconnected (Chapter 8). We do not know the degree of connectivity or its role in the viability of the species, but we assume that connectivity per se is important. We do not know, for example, how population dynamics in Saskatchewan affect those in Montana. In later chapters, however, we demonstrate lagged synchronous fluctuations that resemble the traveling waves produced in predator-prey models that include movement. Thus, we have support for the importance of the connectivity of lynx populations from metapopulation theory, spatial models and, limited empirical data.

We know very little about the densities of snowshoe hares or red squirrels in the contiguous United States, but recognize tremendous variability in these densities among forest types and successional stages. Given this variability, source-sink modeling suggests that landscape proportions, spatial arrangement, and turnover rates of these successional stages may be critically important to the stability of lynx subpopulations.

We suspect that competition from other carnivores could mediate lynx-prey interactions (Chapter 4), and we know that generalist predators can alter the cyclic dynamics of prey populations. But we do not know how these variables are affected by forest fragmentation, nor how they affect lynx demography; we cannot parameterize the simplest model that we might construct of a lynx population. Without better empirical knowledge of the biology of the lynx-prey-vegetation system, these concepts and models can

only guide us in the most general sense. Even so, they provide us with useful, and in some cases the only, guideposts on the path to scientific management of lynx.

Our uncertainty about the ecology of lynx, combined with the obviously complex interactions of cycling populations over an expansive assumed metapopulation structure, make the lynx-prey-vegetation system a complex ecological problem. Several recent conceptual developments, like source-sink and metapopulation theories, clearly have major implications for lynx populations in the contiguous United States; but without more empirical data and modeling efforts, we can only guess at what those are. We know remarkably little about the current status and numbers of lynx in the contiguous United States (Chapter 8). However, what little we know indicates that the subpopulations are not large. Until we better determine the current location and sizes of lynx sub-populations, it is unwise to assume that these populations can be reduced or further isolated without sharply increasing the risk of their individual and collective extinction.

Literature Cited

- Beissinger, S. R. and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821-841.
- Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91-98.
- Blasius, B., A. Huppert, and L. Stone. 1999. Complex dynamics and phase synchronization in spatially extended ecological systems. *Nature* 399:354-359.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.
- Buechner, M. 1987. A geometric model of vertebrate dispersal: tests and implications. *Ecology* 68:310-318.
- Clark, B. K., D. W. Kaufman, G. A. Kaufman, E. J. Finck, and S. S. Hand. 1988. Long-distance movements by *Reithrodontomys megalotis* in tallgrass prairie. *American Midland Naturalist* 120:276-281.
- Cockburn, A. M., P. Scott, and D. J. Scotts. 1985. Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). *Animal Behavior* 33:908-915.
- Cohen, D. and S. A. Levin. 1991. Dispersal in patchy environments: effects of temporal and spatial structure. *Theoretical Population Biology* 39:63-99.
- Dickman, C. R. and C. P. Doncaster. 1989. The ecology of small mammals in urban habitats. II. Demography and dispersal. *Journal of Animal Ecology* 58:119-127.
- Doebeli, M. 1995. Dispersal and dynamics. *Theoretical population biology* 47:82-106.

- Elton, C. and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology* 11: 215-244.
- Erlinge S., J. Agrell, J. Nelson, and M. Sandell. 1991. Why are some microtine rodent population cycles cyclic while others are not? *Acta Theriologica* 36:63-71.
- Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41:300-314.
- Frank, A. S. 1986. Dispersal polymorphisms in subdivided populations. *Journal of Theoretical Biology* 122:303-309.
- Gaines, M. S. and L. R. McClenaghan, Jr. 1980. Dispersal in small mammals. *Annual Reviews of Ecology and Systematics* 11:163-196.
- Gilpin, M. 1991. The genetic effective size of a metapopulation. *Biological Journal of the Linnean Society* 42:165-175.
- Gilpin, M. E. and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19-34 *in* M. E. Soulé, editor. *Conservation biology*. Sinauer Associates, Sunderland, MA.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior* 28: 1140-1162.
- Gurney, W. S. C., A. R. Veitch, I. Cruickshank, and G. McGeachin. 1998. Circles and spirals: population persistence in a spatially explicit predator-prey model. *Ecology* 71: 2516-2530.
- Haggerty, T. M. 1988. Aspects of the breeding biology and productivity of Bachman's sparrow in central Arkansas. *Wilson Bulletin* 100:247-255.
- Hamilton, W. D. and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269:578-581.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210-221.
- Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* 60:353-367.
- Hanski, I., P. Turchin, E. Korpomaki, and H. Henttonen. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* 364:232-235.
- Harrison, S. 1993. Metapopulations and conservation. Pages 111-128 *in* P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large scale ecology and conservation biology*. Blackwell Scientific Publications, Boston.
- Harrison S. and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. *Oikos* 56:293-298.
- Hastings, A. 1983. Can spatial variation alone lead to selection dispersal? *Theoretical Population Biology* 24:244-251.
- Hobbs, N. T. and T. A. Hanley 1990. Habitat evaluation: do use/availability data reflect carrying capacity? *Journal of Wildlife Management* 54:515-521.
- Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181-208.

- Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of 'sink' populations. *Biological Conservation* 57:239-255.
- Krebs, C. J. 1994. *Ecology: the experimental analysis of distribution and abundance*. Harper Collins, New York.
- Krebs, C. J. 1992. The role of dispersal in cyclic rodent populations. Pages 160-173 in N. C. Stenseth and W. Z. Lidicker, Jr., editors. *Animal dispersal*. Chapman & Hall, London.
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. *Conservation Biology* 8:185-195.
- Levin, S., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. *Theoretical Population Biology* 26: 165-191.
- Levins, R. 1969. The effects of random variation of different types on population growth. *Proceedings of the National Academy of Science* 62:1061-1065.
- Levins, R. 1970. Extinction. *Lectures on Mathematics in the Life Sciences* 2:75-107.
- MacArthur, R. H. and E. O. Wilson. 1967. *The theory of island biogeography*. Volume 1. Monographs in population biology. Princeton Univ. Press, Princeton, NJ.
- May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. *American Naturalist* 107:621-650.
- Moss, R, D. A. Elston, and A. Watson. In press. Spatial asynchrony and demographic travelling waves during red grouse population cycles. *Ecology*.
- O'Donoghue, M. 1997. Responses of coyotes and lynx to the snowshoe hare cycle. Ph. D. Dissertation, University of British Columbia, Canada.
- Okubo, A. 1980. *Diffusion and ecological problems: mathematical models*. Springer-Verlag, New York.
- Porter, J. H. and R. D. Dueser. 1989. A comparison of methods for measuring small-mammal dispersal by use of a Monte-Carlo simulation model. *Journal of Mammalogy* 70:783-793.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Pulliam, H. R. and B. J. Danielson 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137:S50-S66.
- Pulliam, H. R., J. B. Dunning, and J. Liu. 1991. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2:165-177.
- Richter-Dyn N. and N. S. Goel. 1972. On the extinction of colonizing species. *Theoretical Population Biology* 3:406-33.
- Ruggiero, L. F., G. D. Hayward, and J. R. Squires. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. *Conservation Biology* 8: 364-372.
- Ruggiero, L. F., R. S. Holthausen, B. G. Marcot, K. B. Aubry, J. W. Thomas, and E. C. Meslow. 1988. Ecological dependency: the concept and its implications for research and management. *Transactions of the Fifty-third North American Wildlife and Natural Resources Conference* 53:115-126.

- Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* 392:491-494.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131-134.
- Shields, W. M. 1987. Dispersal and mating systems: investigating their causal connections. Pages 3-24 *in* B. D. Chepko-Sade and Z. T. Halpin, editors. *Mammalian dispersal patterns*. University of Chicago Press, Chicago, IL.
- Shigesada, N. and K. Kawasaki. 1997. *Biological invasions: theory and practice*. Oxford University Press, New York.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196-218.
- Simberloff, D. 1989. Which insect introductions succeed and which fail? Pages 61-75 *in* J. A. Drake et al., editors. *Biological Invasions: a Global Perspective*. John Wiley and Sons.
- Stenseth, N. C., W., Falck, O. N. Bjornstad, and C. J. Krebs. 1997. Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. *Proceedings of the National Academy of Sciences of the USA* 94: 5147-5152.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.
- Waser, P. M. 1985. Does competition drive dispersal? *Ecology* 66:1170-1175.

