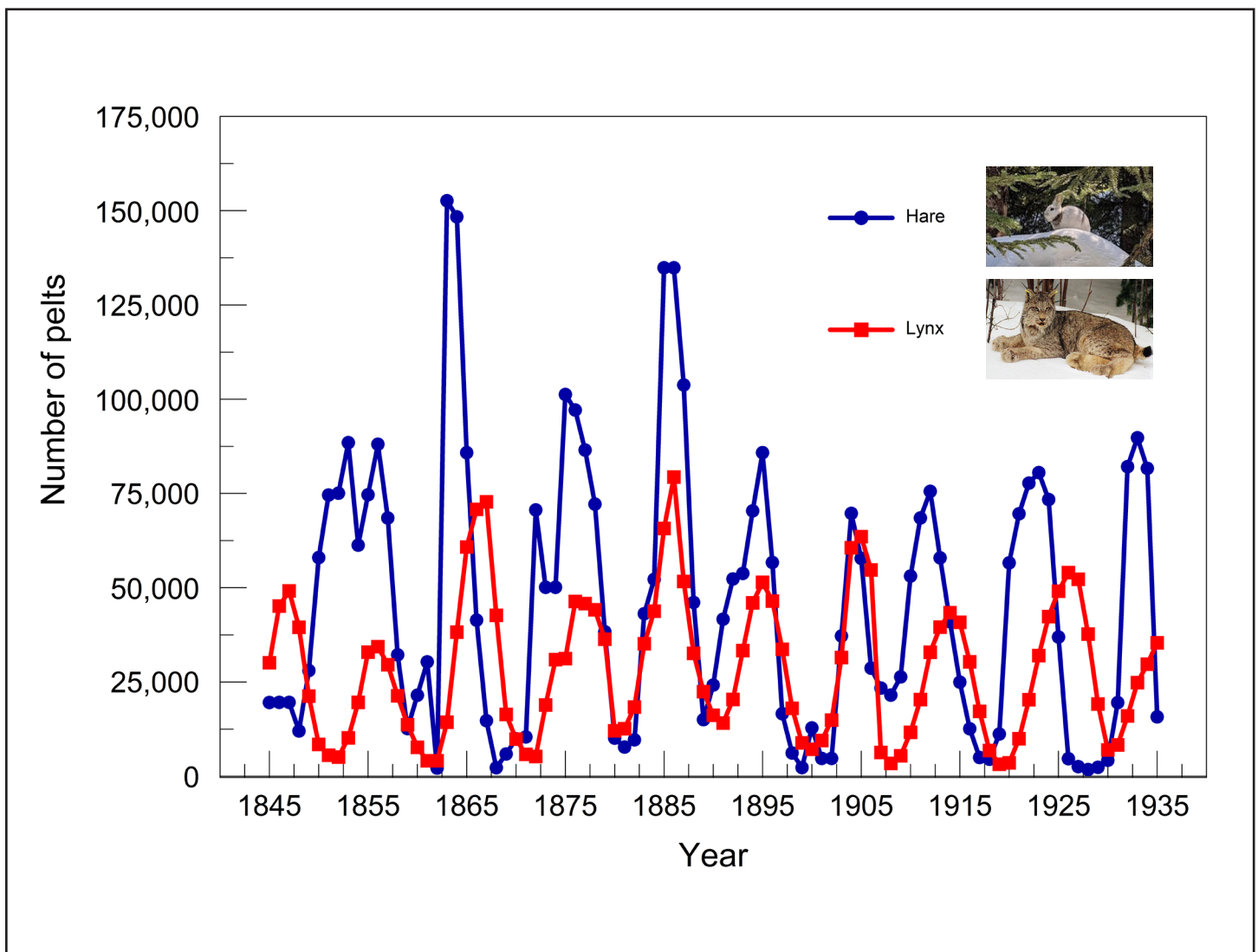


Wild Furbearer Management and Conservation in North America



EDITED BY TIM L. HILLER, ROGER D. APPLIGATE, ROBERT D. BLUETT,
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CHAPTER 5: POPULATION ECOLOGY OF FURBEARERS



Wild Furbearer Management and Conservation in North America

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CHAPTER 5: POPULATION ECOLOGY OF FURBEARERS

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Chapter 5: Population Ecology of Furbearers

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Front cover images courtesy of Amanda Emmel (snowshoe hare [*Lepus americanus*]) and John Organ (Canada lynx [*Lynx canadensis*]); data represent annual number of pelts collected by Hudson Bay Company, Toronto, Ontario, Canada, during 1845–1935, a classic examination of potential population cycles in a predator-prey system, within the limits of the data.

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5

POPULATION ECOLOGY OF FURBEARERS

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Furbearers are a group of wildlife species that ranges across taxonomic classification, including marsupials and rodents, but the group is comprised primarily of carnivores. Life history varies widely, including species of herbivores, omnivores, and carnivores; species that are promiscuous breeders compared to species with well-developed social structure; and mean life span (MLS) ranging from a rodent with MLS of <1 year to large carnivores which have MLS >20 years. Many species of furbearers are managed for harvest primarily for valuable furs, but also other reasons (e.g., food), and some are not harvested, but rather managed as threatened or endangered species.

In this chapter, we review principles of population ecology, concentrating on common models that have been the foundation of understanding population dynamics and that have potential to contribute to population management. Although the basic models of population dynamics will have to be modified or expanded to capture the variation in life history of this diverse group of wildlife, modeling changes in population size can assist managers with selecting appropriate management actions. Our review is not exhaustive, although as much as possible we have used examples that highlight population dynamics of furbearers. In the interest of brevity, in some cases we refer the reader to basic texts such as Rockwood (2006) and Gotelli (2009), or more detailed references such as Williams et al. (2002). With respect to application of basic ecology to wildlife management, our context is the framework described as the North American Model of Wildlife Conservation (Organ et al. 2012, Batcheller and Organ 2024 [Chapter 3]). However, it should be noted that traditional ecological knowledge (Berkes et al. 2000, Voirin et al. 2024 [Chapter 4]) has an important influence on management practices in North America, particularly Canada, and elsewhere in the world.

A population is a group of interbreeding individuals of the same species found in the same space or area. Understanding population dynamics is fundamental to ecology and starts by delineating the space by biologically meaningful boundaries (e.g., a wetland complex or a forested landscape) and the time frame of study. In the case of furbearers, most often the extension

of this fundamental goal is that species are commonly managed for harvest. However, some furbearing species in some areas are protected and not harvested because of low population abundance at local, regional, or larger scales (see Lewis and Weir 2024 [Chapter 8]). From a practical viewpoint, furbearer populations are often delineated by jurisdiction (e.g., management unit, entire state or province). Ultimately, the ability to understand dynamics and model changes in population size allow managers to select appropriate management and conservation strategies, given alternative predictions.

The principles of population ecology have their fundamental underpinnings in studies of humans, microorganisms, and insects, the latter 2 groups partly because they have short generation times and can be propagated in the laboratory. It was not until the early 1900s that principles derived from such studies were adapted to wild vertebrates (Kingsland 1985), stimulated by interest in the natural history of birds (Lack 1966), small mammals (Chitty 1960), and notably, classic predator-prey dynamics of furbearers (Elton and Nicholson 1942). Early on, the economic value of exploited populations of fish motivated important contributions to quantitative models and theory. Historically, both harvest and special protected status of cetaceans and pinnipeds have relied on fisheries population models (Eberhardt and Siniff 1977). Because of the importance of ungulates as harvested animals, there is a long history of assessment and modeling of populations of this taxa (Caughley 1977, McCullough 1979, Boyce 1992, Clutton-Brock et al. 1997).

Most foundational theory and modeling was first developed with respect to the dynamics of individual species, and then expanded based on interest in predator-prey dynamics and interspecific competition. Long-term studies of furbearers have made important contributions to population ecology. We note the detailed, mechanistic studies of interactions between Canada lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*; Keith et al. 1984, Krebs et al. 2001), and population dynamics of muskrats (*Ondatra zibethicus*; Errington 1963) and gray wolves (*Canis lupus*; Fuller et al. 2003), although conservation and harvest-management challenges have stimulated recent research on a wide range of species.

DENSITY-INDEPENDENT POPULATION GROWTH

Continuous-Time Principles

A fundamental principle of ecology is that without environmental resistance, populations tend to grow exponentially (i.e., density-independent growth; Turchin 2001). Although exponential growth is ultimately simplistic because populations exhibit self-limitation or fluctuations, it is a useful starting point for quantitatively describing population dynamics.

In any well-defined population, the change in population size (ΔN) is a function of the number of births (B), deaths (D), immigrants (I), and emigrants (E). Although movement into and out of populations has received much attention during the past 20 years (Hanski 1999), classic models of growth assumed that populations were closed (Williams et al. 2002) with respect to I and E .

The first mathematical models considered growth of large, continuously breeding populations such as humans and microbes (Kingsland 1985), sometimes referred to as birth-flow populations (Rockwood 2006). The differential equation,

$$\frac{dN}{dt} = rN, \quad (1)$$

describes the instantaneous growth of N , where $r = (b - d)$ is the instantaneous per capita birth rate (b) minus the instantaneous death rate (d). Note that the net per capita rate of increase,

$$\frac{dN}{dt} / N = r, \quad (2)$$

is a constant. In these instantaneous-time models of large birth-flow populations, the assumption is that the sequence of individual births and deaths is essentially a continuous random process (i.e., a Poisson random process; see Williams et al. 2002), enabling the integrated solution to Equation 1 to describe the population trajectory,

$$N_t = N_0 e^{rt}. \quad (3)$$

Discrete-Time Models

Any useful model must be appropriate to the life history of the organism of interest, and ecologists have modeled populations differently if the organism has overlapping generations (Rockwood 2006). Furthermore, many species, including furbearers, breed within a relatively brief birth-pulse period (Caughley 1977) and, in practical terms, are often surveyed once/year. In such cases, it is appropriate to use a discrete-time (difference equation) representation of the rate of change of the population with a unit time step ($\Delta t = 1$):

$$\frac{N_{t+1} - N_t}{1} = \frac{\Delta N}{1} = R_1 N_t. \quad (4)$$

Equation 4 defines discrete, geometric, density-independent population growth, where R_1 represents net growth/unit time (e.g., 1 yr). Starting with an initial population size of N_0 , the solution to this difference equation is:

$$N_t = N_0 (1 + R_1)^t. \quad (5)$$

This discrete form is usually presented in a slightly different form:

$$N_t = N_0 \lambda^t, \quad (6)$$

where λ is the finite rate of growth/year. Note that the population increases if $\lambda > 1$, decreases if $\lambda < 1$, and is stationary if $\lambda = 1$. These models are useful in general terms, as long as we recall the simplistic assumptions of: a) constant environment, b) no genetic structure, c) stable age and sex structure, and d) growth with no time lags. By noting the relationship between Equations 3 and 6, we can estimate $r = \ln \lambda$. Two assumptions (a and d) are particularly relevant to the equivalence of r and λ . It is correct to interpret λ as the finite rate of growth of a population, though it is important to realize that strictly it assumes a large birth-flow population with a constant b and d throughout the interval (Caswell 2001). Comparing Equations 5 and 6, we note $\lambda = (1 + R_1)$. Since most furbearing species have a birth-pulse life history, and in practical terms are surveyed only once/year, it is natural to think in terms of these discrete parameters (Williams et al. 2002). From a time series of N_t , a biologist might obtain an initial approximation of R_1 or λ , and perhaps even calculate a variance of the parameter by assuming the years were independent. For short-lived species (e.g., muskrats) for which annual reproduction substantially influences population dynamics, R_1 is sometimes interpreted as reflecting the spring–fall proportional increase (Errington 1963), although this does not fully address subsequent mortality.

These exponential models were first used to describe explosive growth of insect and microbe populations. We emphasize that biologists applying them to vertebrate populations must be explicit about the equivalence and interpretation of the parameters depending on the source of data, whether the specific model that was applied included assumptions of continuous or discrete time, and how the model corresponds to the life history of the species. Often, the estimated parameters are used in a comparative sense (Promislow and Harvey 1990) to understand relationships among reproduction and mortality among species exhibiting so-called fast and slow life histories (Oli and Dobson 2003). However, specific estimates of r or λ and MLS are fundamental to conservation and management. As illustrated by Fuller et al. (2003), even large mammals (e.g., gray wolves) exhibit a wide range of rates of increase depending on environmental conditions. It is often true that mammal populations exhibit the most explosive growth when invading unoccupied regions. For example, the Idaho Legislative Wolf Oversight Committee (2002) reported that after reintroduction of 15 gray wolves in Idaho, USA, the population increased to 261 individuals in 6 years, which is $\lambda = 1.61$ ($r = 0.476$). In comparison, Devenish Nelson et al. (2010) analyzed

data from populations of the much smaller red fox (*Vulpes vulpes*) in Australia and in the U.S., and estimated average rate of growth as $\lambda = 1.08$, $r = 0.077$, and $R_1 = 0.08$. At the fast extreme of the spectrum of life histories for furbearing species, Clark (1987) estimated average $\lambda = 2.86$, $r = 1.051$, and $R_1 = 1.86$, among muskrat populations along the Mississippi River in Iowa, USA.

DENSITY-DEPENDENT GROWTH

Linear Density Dependence

Populations do not maintain unlimited growth forever. The effects of predation, disease, and competition may increase more intensely at higher population densities, and realized population growth eventually declines. The simplest model to describe density dependence assumes intraspecific competition results from limited resources that influence per capita rates of birth, death, and dispersal. For example, among muskrats, intraspecific exploitive or contest competition (Rockwood 2006) for food and cover that is secure from predation affects body condition, reproduction, and survival rates (Virgl and Messier 1997). In highly territorial species (e.g., gray wolves), competitive interactions are often by more direct interference (Cubaynes et al. 2014) rather than simple depletion (Rockwood 2006). Although not mechanistically detailed, in these models, population size (N) reaches a carrying capacity (number of individuals [K]) in relation to the limiting resources as a simple linear decline in the per capita rate of growth as the population approaches K (Verhulst 1838, Pearl and Reed 1920, Lotka 1925):

$$\frac{dN}{dt} / N = r_{dd} = r_{max} \left(1 - \frac{N}{K} \right) . \quad (7)$$

Here, we express the realized density-dependent per capita growth rate (r_{dd}) as a function of the maximum per capita growth that would be expressed under the assumption of density independence (r_{max}). When N is near zero, the population will grow at essentially the maximum per capita rate; when N approaches K , the realized net per capita rate is reduced to near zero. If by some means the population exceeds carrying capacity ($N > K$), the term in parentheses in Equation 7 is negative and the population declines toward K .

The differential equation form of the logistic is generally more easily recalled than the integrated form:

$$N_t = \frac{K}{1 + \left(\frac{K}{N_0} - 1 \right) e^{-rt}} , \quad (8)$$

where N_0 is initial population size and r is the actual growth rate estimated over a specified time period t . The parameters r and K can be estimated by a variety of means (Williams et al. 2002), but a simple linear regression of the $dN/(dt \times N)$ (i.e., per

capita rate) as a function of N yields a reasonable initial approximation of r (i.e., y-intercept) and K (i.e., x-intercept). This logistic model assumes that: a) carrying capacity is constant (the environment does not change stochastically), b) the age and sex structure of the population does not affect population growth (essentially all individuals are equivalent), c) per capita rates of birth and death change linearly as density increases, and d) the rates respond instantaneously to changes in the ratio of N/K (i.e., there are no time lags).

A discrete-time model that expresses growth with linear density dependence can be derived algebraically (Rockwood 2006:37):

$$N_{t+1} = \frac{RN_t}{1 + \frac{(R-1)(N_t)}{K}} , \quad (9)$$

Note that when N_t is near zero, the population grows at essentially the maximum rate (R), and when N_t reaches K , $N_{t+1} = N_t$. This formulation is known as the Beverton-Holt model and has made historically important contributions to the theory of exploitation, especially of fish populations (Beverton and Holt 1957). Similar concepts and models have been applied to marine mammals (Eberhardt and Siniff 1977), and ultimately to terrestrial mammals. For example, Korablev et al. (2011) acceptably fit a version of the logistic model to the growth of a population of European beavers (*Castor fiber*) using data collected during the 72 years after an initial reintroduction of 5 individuals in 1936 (Fig. 5.1). However, this population fluctuates around estimated carrying capacity because of non-linear and time-lag effects.

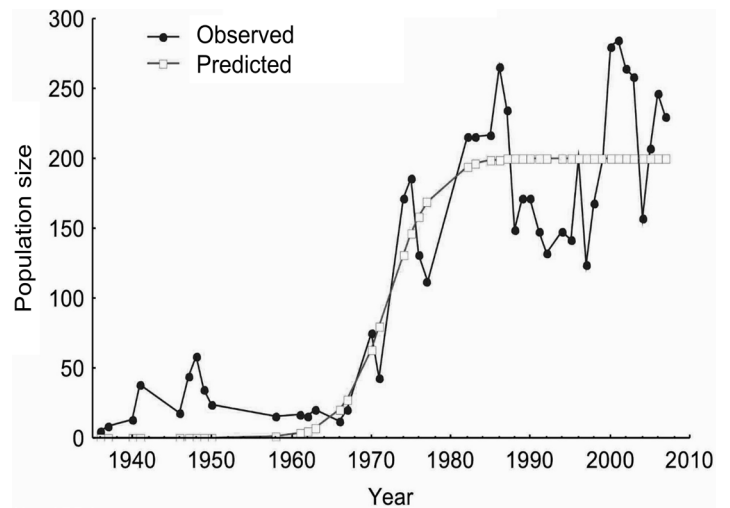


Fig. 5.1. Observed and estimated population sizes of European beavers (*Castor fiber*) in the Upper Volga Basin, Russia, during 1936–2010; reintroduction of 5 individuals occurred in 1936 (Korablev et al. 2011; figure used with permission).

Non-Linear Density Dependence

As the above example about European beavers demonstrates, although there are many examples of fitting data to the logistic model, the assumption of linear density dependence is too restrictive. There is abundant evidence that birth and death rates among many long-lived species, including some furbearers, are related to density in a non-linear manner (Fowler 1987, McCullough 2001). For example, Gerber et al. (2004) reported a decline in the per capita rate of population increase (r) in sea otters (*Enhydra lutris*) along the coast of Washington, USA, from $r = 0.2$ at a population size of 100 individuals to $r = 0$ at a population size of 600. In social species (e.g., gray wolves), combinations of maternal condition of females and behavioral adaptations associated with pack size resulted in non-linear density dependence in both reproduction and survival (Stahler et al. 2013). An early way to incorporate non-linear effects into simple models was recognized by Gilpin and Ayala (1973), who modified Ricker's (1975) discrete form of the logistic model by incorporating a superscript parameter (θ) on the ratio of density relative to carrying capacity:

$$N_{t+1} = N_t e^{r_{max} [1 - (N_t/K)^\theta]} \quad (10)$$

When $\theta = 1$, the density effects are linear and the rate of change of the population size is symmetrical, reaching a peak at $N = K/2$. When $\theta > 1$, density dependence is strong even at low population densities, a condition termed overcompensation. In such populations, the curve of rate of change is skewed and reaches the maximum at $< K/2$. When $\theta < 1$, density dependence has little effect at low population density, a condition known as undercompensation, and maximum rate of growth is not reached until fairly close to K (Williams 2013; Fig. 5.2A). Overcompensating populations grow very quickly toward K , frequently exceed K , and often fluctuate erratically around K . Undercompensating populations grow gradually toward K , and generally fluctuate moderately about K . Accounting for nonlinear density dependence can have implications for harvest management of furbearers and other species given that the density at which predicted yield is highest differs from the assumptions of linear density dependence (Williams 2013; Fig. 5.2B).

Observed Population Fluctuations Compared to Model Results

The basic models for exponential and logistic growth are useful for initially understanding dynamics, but observed fluctuations in populations of most furbearing species do not seem to follow the assumptions of these simple models. Departure from the predicted population dynamics can be a result of actual biological variability in the process (e.g., genetic differences among females resulting in differences in litter size) or uncertainty in the observed average value of a population parameter (e.g., sampling variation in mean and standard deviation of litter size).

A first step in modeling population fluctuations is often to incorporate variance in parameters into the model, but sometimes it is necessary to consider an alternative model that better fits the situation. For example, substituting \bar{r} in Equation 3 and considering the

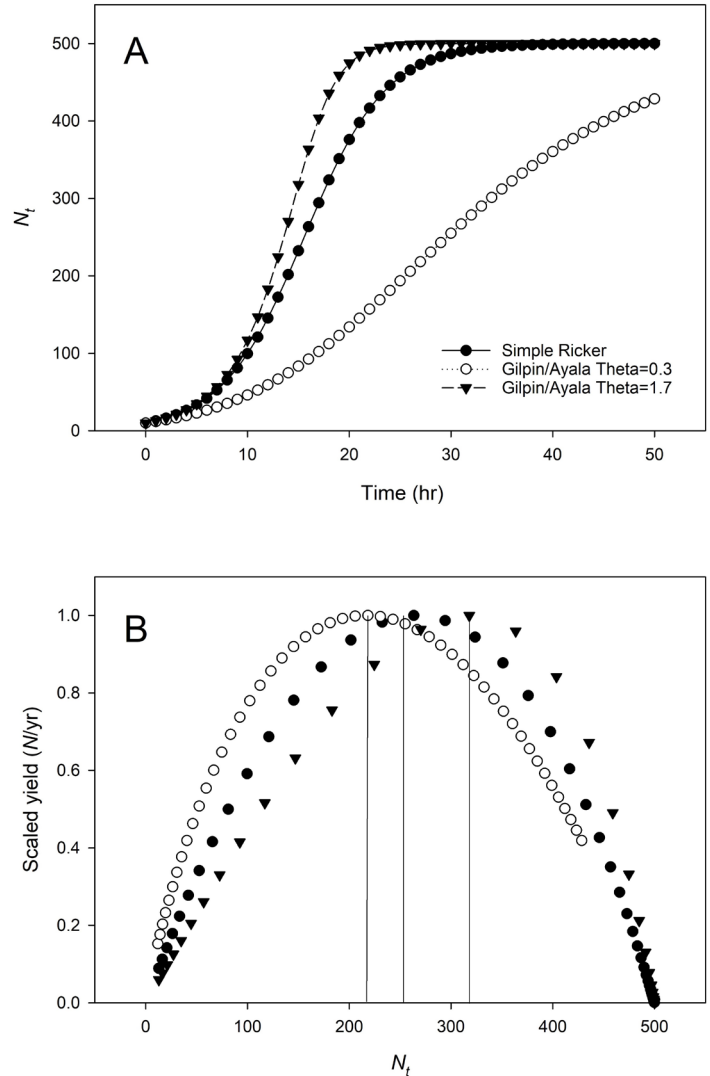


Fig. 5.2. Comparison of A) population growth and B) annual scaled yield among the Ricker (1975) logistic growth model and modifications using the Gilpin and Ayala (1973) adjustment with $\theta = 0.3$ and $\theta = 1.7$. Data shown for a hypothetical population with a carrying capacity ($K = 500$), and a potential per capita growth rate ($r = 0.25$). In B, yield (N/yr) is scaled by dividing annual yield by the maximum yield under that model. Vertical lines represent population size at which yields are maximized. The population size at which yield maximizes for the simple Ricker response is 250, whereas the yield maximizes at 218 and 317 for $\theta = 0.3$ and $\theta = 1.7$, respectively.

associated $\text{Var}(\bar{r})$ will produce changes in \bar{N}_t that vary from smooth exponential growth to trajectories that do not seem exponential at all. This simple change in the model has resulted in a rule of thumb used in population viability analyses for small populations that if $\text{Var}(\bar{r}) > 2\bar{r}$, then extinction is likely (Gotelli 2009).

Variation in potential for fluctuations may also be related to the relative demographic stochasticity among different life histories of species. For example, consider 2 species with net $\bar{r} = 0.05$;

the first species with $b = 0.55$ and $d = 0.50$, and a second species with $b = 1.45$ and $d = 1.40$. When substituting \bar{r} in Equation 3 with the same $\text{Var}(\bar{r})$ for both species, the population of the second species will be >2.5 times more variable compared to the population of the first species. Although instructive, both examples are still based on the framework of the exponential model that were envisioned for larger populations, whereas a completely different discrete-process model might more realistically represent the situation for very small populations where a clustered sequence of reproductive failures can readily cause extinction (Morris and Doak 2002).

With respect to density-dependent population growth, as illustrated above, short-lived and long-lived species generally respond to increasing density over different time frames, resulting in different non-linear patterns. Long-lived species (e.g., wolverines [*Gulo gulo*]) may not show strong density dependence until population size is relatively close to K , undercompensate, and approach K more gradually. Short-lived species (e.g., muskrats) respond to density at low population levels, overcompensate, and may exceed K . However, in neither of these life-history examples do these species respond to population density in the instantaneous fashion, which is a general assumption associated with the models. More realistically, the populations respond with a time delay (τ), i.e., to density at some time in the past ($N_{t-\tau}$). We can modify the logistic model, in this case Ricker's (1975) original discrete logistic with $\theta = 1$ (Equation 10), to illustrate the concept (Rockwood 2006):

$$N_{t+1} = N_t e^{r_{max} \left(1 - \frac{N_{t-\tau}}{K}\right)}, \quad (11)$$

The dynamics now depend on $r_{max} \times \tau$ (May and Oster 1976). Intuitively, it makes sense that species with large r_{max} and delayed response to intraspecific competition would fluctuate widely in abundance, though the range of r among actual populations of furbearers is much less than the values simulated in theory (May and Oster 1976). Furthermore, the discrete form of the logistic that is often appropriately used to model populations of furbearing species with distinct seasonal birth pulses has an implicit time lag of 1. Thus, in the discrete model with large r , modeled dynamics can exhibit cycles or even chaos where there is no repeating pattern in the fluctuations. In general, adding variance to only r results in smaller average population size, and therefore much longer time to reach K compared to the deterministic model. Population dynamics in response to random variation in K not only depend on the strength of density dependence, but especially on the value of r . A population with large r tends to track the fluctuations in K , whereas a population with small r tends to follow the running average of fluctuating K (May and Oster 1976, Morris and Doak 2002, Rockwood 2006).

Clearly, the life-history characteristics across the spectrum of species, such as muskrats, northern raccoons (*Procyon lotor*), and gray wolves, will necessitate careful consideration of the importance of density dependence, environmental variation, and time lags in modeling population dynamics. Combining these factors complicates developing a useful density-independent or density-dependent model (McCullough 2001). Certainly, simple models can incorporate variability and be altered to mimic the chaotic fluctuations that

are observed in natural systems. Biologists and managers should recognize the value of the basic models as starting points and collect data to incorporate appropriate ecological details into the models to make them most useful.

AGE-STRUCTURED POPULATION MODELS

Prior to this section, we have discussed population models that either ignore or include strong assumptions about the complex age structure that is common among most furbearing species. Like the models above, much of the theory of age-structured population models was first developed for human populations and then adapted to the study of animals (Deevey 1947). In practice, furbearer biologists frequently start with data on the age structure and age-specific reproductive rates, which were often derived from samples of the age structure of harvested individuals (Downing 1980).

Survivorship (l_x) is the number (often standardized on initial cohort of 1,000) or proportion (if standardized on 1.0) of individuals that survive to age x . In analyses of life tables derived from age structure, the age-specific survival rate (S_x); the probability that an individual aged x will survive to age $x+1$ is estimated as $S_x = l_{x+1}/l_x$. As Groenendijk et al. (2014) reported for giant otters (*Pteronura brasiliensis*) in Peru, long-lived furbearing species often have relatively high levels of age-specific mortality at younger ages, after which survival is relatively high (Fig. 5.3). In many field studies of furbearers, S_x is estimated directly using radio-marked individuals or by collecting data on cohorts of marked animals (Williams et al. 2002). Age-specific fertility is more complicated to define because, strictly speaking, most of life-table theory was based on continuous ages and time, whereas age classes are discrete. In life-table usage, age-specific reproductive rate (m_x) is defined as the number of female offspring born/female from age x to $x+1$. In the projection-matrix context, and with the provision that we align sampling with the birth pulse (i.e., age and time are on the same renewal date), fertility (F_i) is the number of female offspring born/female of age i to $i+1$ that will be survive to time $i+1$ (Noon and Sauer 1992, Williams et al. 2002).

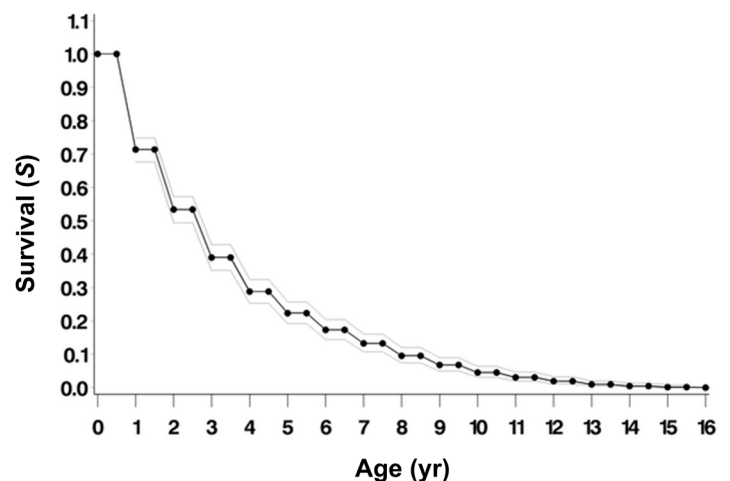


Fig. 5.3. Survivorship from birth to death of all cohorts of male and female giant otters (*Pteronura brasiliensis*; $n = 177$) in Peru. Figure modified from Groenendijk et al. (2014).

Projection Matrices

Leslie (1945) developed the method of using a matrix of age-specific fertility and age-specific survival, along with a vector of individuals of each age class, to project population change 1 year at a time. Projection matrices (Caswell 2001, Morris and Doak 2002) derived from field data collected by wildlife biologists are now increasingly used to assess population dynamics, in part because they provide an intuitive way to visualize the effects of both reproduction and survival data. It is often assumed that the proportion of each age class in the harvest is equal to the proportion of each age class in the population, so the sample is viewed as representative of the numbers in age classes n_1, n_2, \dots . However, for a variety of reasons (e.g., differing harvest vulnerability), young-of-the-year may be either underrepresented or overrepresented in harvest data, complicating estimates of n_0 . Examining reproductive tracts from harvested animals provides rates m_1, m_2, \dots . When the sample is from harvest data and n_0 is poorly known, it is appropriate to view the survey as before the birth pulse for young-of-the-year (Noon and Sauer 1992), where the appropriate matrix for 3 age classes is:

$$A = \begin{bmatrix} S_0 m_1 & S_0 m_2 & S_0 m_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{bmatrix}. \quad (12)$$

Note that fertility (F_i) is the product of the age-specific reproduction by each age class (m_i) and the survival probability of young-of-the-year (S_0). This structure can be applied to furbearing species where it is very difficult to observe young-of-the-year in the field (e.g., bobcats [*Lynx rufus*], Canada lynx, mustelids). It is important to note that for species such as muskrats, which have >1 litter/year, the probability of pregnancy and differences between or among litter sizes must be appropriately combined into a total for the breeding season (Clark et al. 2008).

Furbearing species such as canids are longer-lived, and the number of young-of-the-year might reasonably be observed directly, similar to bears (*Ursus* spp.). A post-breeding formulation of the matrix is appropriate for such species, in which the sample size used to estimate age-specific rates for older age classes is often small. Thus, it is often necessary to combine age classes. Such matrices are known as stage-based matrices and generally can be analyzed similar to the traditional Leslie matrix (Caswell 2001, Williams et al. 2002). In Equation 13, m_3 is the reproductive rate of age class 3 and older females, and S is the probability of survival of females among the pooled samples of the oldest age group (Caswell 2001):

$$A = \begin{bmatrix} S_0 m_1 & S_1 m_2 & S_2 m_3 & S m_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & S \end{bmatrix}. \quad (13)$$

Here, we have presented basic models that use separate demographic estimates from field data as the basis for the analyses of the potential long-term dynamics of the population. Note that we have not considered approaches that integrate the estimation of parameters into a single analysis (Fieberg et al. 2010). For the analyses we present, the properties of the population are derived from the characteristic equation of the matrix, which summarizes density-independent growth once a population has reached a stable-age distribution. The dominant eigenvalue of the matrix is the finite rate of change (λ), and the eigenvectors associated with the dominant eigenvalue are the stable-age distribution (n_x) and the reproductive values (v_x ; Caswell 2001, Williams et al. 2002).

It is beyond the scope of this chapter to present a detailed mathematical example, but several software packages exist for estimating these population characteristics (e.g., Morris and Doak 2002), including functions that are part of Excel (Microsoft, Redmond, Washington, USA) and analytical frameworks (e.g., package popbio [Stubben and Milligan 2007] in Program R [R Core Team 2023]; MATLAB [MathWorks, Natick, Massachusetts, USA]). Matrix analyses have been widely used to integrate demographics (Caswell 2001, Morris and Doak 2002), to understand how variation in vital rates contributes to variation in λ (Slade and Levenson 1982), and to evaluate conservation and management strategies (Morris and Doak 2002, Harding et al. 2001, Macdonald et al. 2009, Devenish Nelson et al. 2010, Sæther et al. 2010).

A useful extension of the mathematics is to study the sensitivity and elasticity, i.e., the relative influence of changes in fertility (F_i) and survival (S_j), on the potential rate of growth (λ) of the population (Caswell 2001, Macdonald et al. 2009). For example, a biologist might have the goal to quantitatively understand how sensitively λ will respond to a proposed increased level of harvest that might be hypothesized to decrease annual S by 5%. Alternatively, a biologist managing a species of concern might want to evaluate the relative magnitude of increases in population rate of growth among several protection alternatives that could influence S or F (Morris and Doak 2002). The sensitivity analyses can be extended to the lower-level components of the matrix elements (Noon and Sauer 1992, Caswell 2001, Clark et al. 2008). For example, as formulated in the above matrices, fertility (F_i) is a product of survival (S_j) and age-specific reproductive rate (m_j), and the latter is a product of the lower-level parameters of pregnancy rate and litter size (i.e., $m_j = pr_j \times ls_j$). Sensitivity analyses performed in this way generally confirm that pregnancy rates, particularly among first-time breeders, contribute more substantially to variation in λ than does variation in litter size (Todd and Keith 1983, Clark and Fritzell 1992, O'Donoghue et al. 1997).

As an example, we present analyses incorporating data on reproduction and survival, and estimates of variation in these vital rates, into a population projection model of bobcats (Gosselink et al. 2011). Gosselink et al. (2011) calculated the asymptotic finite rate of increase (λ), the stable-stage distribution (n_x ; expressed as the proportion of individuals in each stage), the vector of reproductive values (v_x ; relative contribution of females

of each age class), and the generation time (T [yr]; average interval of first reproduction between mothers and daughters) of populations described by the matrix using MATLAB (Morris and Doak 2002). The authors then incorporated uncertainty in reproductive parameter estimation by selecting each vital rate at random from a normal distribution (Caswell 2001), with the observed mean and standard deviation (e.g., mean litter size and SD[litter size]). To incorporate variation among years and to account for potential covariation, they first created matrices with observed vital rates and then randomly selected among these new matrices each year (Morris and Doak 2002) of the 15-year projection, a practical planning time for wildlife managers. They calculated an estimate of λ and 95% bootstrap probability limits of that estimate by resampling 1,000 bootstrap replicate projections. With this approach, they estimated $\bar{\lambda} = 1.085$ with a 95% confidence interval of 0.993–1.193 (Gosselink et al. 2011). The stable-stage distribution was weighted to young ages: 53% young-of-the-year (0–1 yr), 28% yearlings (1–2 yr), and 12% intermediate adults (2–3 yr), and only about 7% older adults (≥ 3 yr). Reproductive values (the proportional contribution of each age class to production of female offspring into the future) increases with age, emphasizing the importance of females older than stage class 3 years (i.e., $v_0 = 10\%$, $v_1 = 13\%$, $v_2 = 13\%$, $v_3 = 11\%$, $v_4 = 15\%$, $v_5 = 18\%$, $v_6 = 20\%$).

In recent decades, simple analytical models such as those described above have become widely used in population viability analyses and predicting the consequences of management actions (Caswell 2001, Morris and Doak 2002). Now, there is a large amount of literature encompassing more sophisticated projection modeling that incorporates uncertainty and especially density-dependent feedback on reproduction and survival. Sometimes the matrix-analytical techniques described above can be applied to more sophisticated models that realistically simulate population dynamics (Caswell 2001), but there is considerable debate on how much realism is appropriate to management decisions (Beissinger and Westphal 1998, Coulson et al. 2001). Stephens et al. (2002) compared results and predictions from models ranging from a 6-stage population-based matrix with uncertainty to models that included behavioral responses to density-dependent availability of breeding sites and winter survival parameterized for alpine marmots (*Marmota marmota*) in southern Germany. Relatively simple matrix models were adequate for making predictions about population size only under equilibrium conditions, but transient dynamics could be predicted only by incorporating more detailed behavioral and spatial effects (Stephens et al. 2002).

SPATIALLY STRUCTURED POPULATIONS

The concepts and models we have introduced above are based on the assumptions of large panmictic populations occupying continuous habitat. However, habitat conditions often vary subtly in space, so it is more realistic to view populations as panmictic clumped (Fig. 5.4), assuming that there are no mating restrictions based on behavior or distances among individuals. Many common,

widespread furbearing species would be characterized as strongly linked through dispersal, and therefore panmictic, even if habitat conditions vary spatially. Even so, population ecologists are increasingly adding structure to models that incorporate spatial and temporal variation in habitat quantity and quality, and landscape features such as edges, corridors, and spatial configuration of habitat (Fahrign and Merriam 1994, Hanski 1999).

Characterizing Dispersal

There are numerous studies of home ranges of furbearers, and studies of behavioral interactions related to sex, age, and timing of dispersal, but relatively few studies of long-distance dispersal and settling to breed (for information on individual furbearing species, see Chapters 27–66 [Hiller et al. 2024]). In the past, most studies of movements of furbearers employed telemetry, although landscape-genetic techniques are being increasingly used. In a comparative life-history sense (Turchin 1998), range expansion can be rapid for species such as muskrats, which have high r and reported rates of expansion of 10–20 km/year (6–12 mi/yr). For species such as gray wolves, which generally have lower r and strong social structure, a much slower rate of expansion (e.g., 5.5 km²/generation [2.1 mi²/generation]) has generally been observed (Turchin 1998). However, this rate depends strongly on relative availability of unoccupied habitat. Genetic analyses have provided data suitable for estimating rates of diffusion across relatively uniform landscapes at large spatial scales, but now also are used to characterize finer-scale potential dispersal linkages across complex and fragmented landscapes (Cushman et al. 2006, Reding et al. 2013, Reding et al. 2023 [Chapter 16]).

Source-Sink Population Concepts

As amount of habitat decreases or becomes more fragmented, landscapes may essentially be comprised of habitat patches within the surrounding non-habitat matrix (Pulliam 1988, Hanski 1999), which often results in source-sink populations (Fig. 5.4). Furthermore, habitat conditions within some patches are sufficient to maintain subpopulations with $\lambda_{S0} > 1$, whereas sink habitat consists of subpopulations with $\lambda_{Si} < 1$. To quantify the dynamics of a source-sink population, the net per capita rates (i.e., both λ_{S0} and λ_{Si}), and the carrying capacity of the source population (K_{S0}), must be estimated. Most importantly, this would include the movement rates from source to sink subpopulations and vice versa (number of dispersers/total population size/time).

In general, until the population in the source habitat reaches K_{S0} , that subpopulation increases exponentially, whereas the subpopulation in the sink habitat decreases exponentially. Depending on the relative magnitude of the rates of dispersal and growth, at equilibrium the entire population may persist even though there may be more individuals in the unsuitable patches considered to be sink habitat. Therefore, observing high population density in unsuitable habitat may be misleading to the manager because it is dependent on immigration from source subpopulations (Van Horne 1983). Although assessing source-sink population dynamics requires intensive effort of marking animals in multiple

patches of habitat, there are now many applicable extensions to the statistical models of Jolly-Seber to estimate movement rates among multiple patches (Williams et al. 2002). Detailed studies of muskrats have quantified density dependence in reproduction, survival, and movement rates in source-sink populations (Clark and Kroeker 1993, Virgil and Messier 2000).

Not long after the development of matrix models, human demographers modified the mathematics to account for migration among subregions (Caswell 2001). With the increasing interest in spatially structured populations, ecologists have applied similar structures to animal populations (Fahrig and Merriam 1985), including furbearers (Novaro et al. 2005, Maletzke et al. 2015). Such models have heuristic appeal because it is easy to visualize the separate parameters for survival (S_j) and dispersal (d_j). It is straightforward to construct a matrix where movement of subadult classes is unidirectional from source-to-sink subpopulations in contrast to a population with movement in both directions between source and sink subpopulations (and with subpopulation-specific immigration and emigration rates).

In cases of migration in both directions, the overall rate of population growth will be intermediate between the subpopulations, weighted by the exchange rates between source

and sink subpopulations. Combined with data on the relative area used by source and sink subpopulations, and the spatial distribution of each which affects rates of dispersal, managers could investigate whether the amount or strategic placement of source habitat is more effective at maintaining an overall positive rate of population growth. Such models could also help to define spatially explicit harvest regulations that protect source populations while taking advantage of doomed surpluses immigrating into areas of sink habitat. In recent years, the use of genetic technology has enhanced the ability to identify source and sink populations and to inform harvest management (Andreason et al. 2012, Sacks et al. 2016).

Metapopulation Concepts

In landscapes and regions where patches are either occupied or unoccupied, ecologists and evolutionary biologists use the term metapopulation to describe subpopulations that are loosely linked by dispersal (Hanski 1999), though among mammals there is a gradation between source-sink dynamics and metapopulation structure (Elmhagen and Angerbjörn 2003; Fig. 5.4). The dynamics of the overall population are affected by rates of migration and extinction, which in turn are a function of local population size. Highly fragmented landscapes result in lower probabilities of

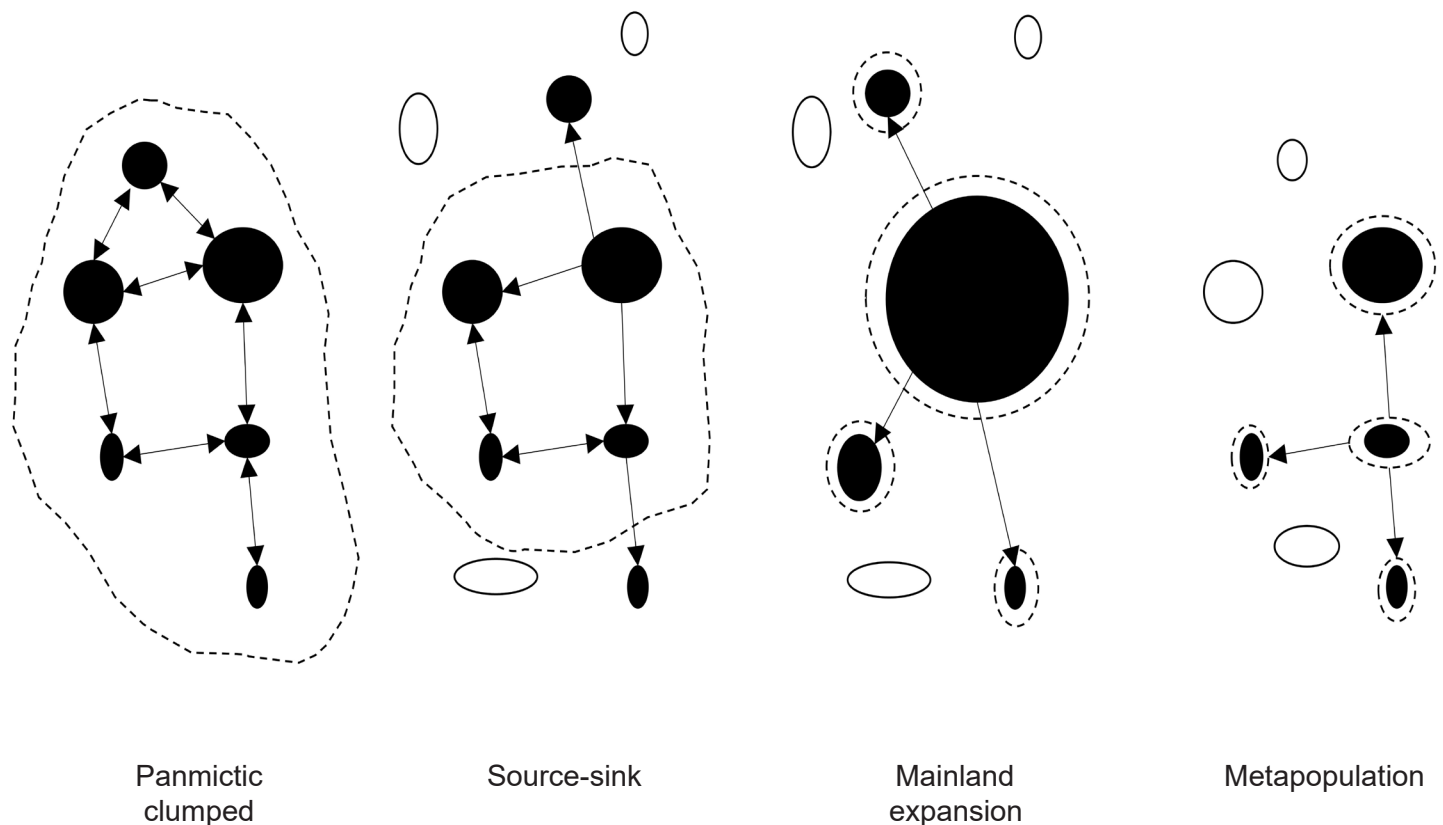


Fig. 5.4. Spatially structured populations, including panmictic clumped, source-sink, mainland expansion, and metapopulation. Dotted lines indicate relative boundaries of population(s), arrows indicate direction of movement, and polygons indicate colonization status (black = colonized, white = uncolonized). Figure based on Vandermeer and Goldberg (2003).

emigration between patches, and populations are prone to extinction in small patches so that the persistence of the metapopulation is low. For example, Schooley and Branch (2009) concluded that the metapopulation theory was useful in conservation planning for round-tailed muskrats (*Neofiber alleni*), but the area-isolation paradigm had to be modified to account for landscape heterogeneity and cost-distance modeling of dispersal. Benson et al. (2019) reported that isolation of mountain lions (*Puma concolor*) resulted in low survival because of effects of inbreeding, but that could be counteracted by relatively low numbers of immigrants enabled by corridor formation with neighboring subpopulations.

On the other end of the management spectrum, Sacks et al. (2016) reported that efforts to eradicate nonnative subspecies of red foxes from regions in California were hampered by high immigration rates from neighboring regions. Conner et al. (2008) concluded that lethal control of coyotes (*Canis latrans*) could be targeted using spatially structured models. Increasingly, models based on metapopulation theory have become useful tools for population analyses essential for regulating harvest of common furbearing species and planning conservation of endangered furbearing species.

PREDATION AND COMPETITION

Interactions between carnivores and their prey have had a strong historical influence on population ecology. Of course, antagonistic attitudes toward large predators led European settlers to exterminate species such as gray wolves and mountain lions from much of North America. Fascination with population cycles of snowshoe hares and Canada lynx that was based on Hudson Bay fur-trading records has been present since the beginning of the science (Elton and Nicholson 1942, Keith 1963), although more recent analyses are much more sophisticated than early observations (Erb et al. 2001). Conflicting viewpoints ranging from control to protection of ecosystem integrity have had a major influence on furbearer management. Here, we briefly outline the extensive literature on the theoretical details of multi-species interactions, with an emphasis on aspects that are relevant to furbearer management.

Initially, predator-prey theory was based on studies of a single pair of species in isolation (Lotka 1925, Volterra 1926), with models based on assumptions similar to Equation 1 above; i.e., in the absence of a predator, the prey population grows exponentially; in the absence of prey, the predator population declines exponentially; and the number of prey consumed/predator is a simple function of random encounter. The fact that the dynamics of the Lotka-Volterra models mimic the observed numerical fluctuations in predator-prey systems led early ecologists to conclude that such interactions were inherently oscillatory. Although the simplistic models have always been criticized, they stimulated substantial laboratory and field research. In fact, even early experiments that examined the dynamics of Lotka-Volterra systems revealed the importance of spatial heterogeneity and dispersal rate in enabling equilibrium rather than oscillations (Gause 1934, Huffaker 1958).

Ecologists then shifted from observation of the pattern of numerical fluctuations to observations and experiments that focused on understanding the mechanisms of predation.

For example, behavioral ecologists recognize that predators searching for, capturing, handling, and digesting prey items requires time and energy that eventually limit the predation rate. Experiments by Holling (1966) explored the changes in per capita rate of predation (number of prey consumed/predator/unit time) as a function of prey density, which he termed the functional response of a predator. Recall that the original Lotka-Volterra model includes the assumption of random encounter so that the per capita rate of predation never reaches an asymptote, which is described as a Type I functional response (Fig. 5.5). Limitation of the prey population is possible because the proportion of the prey population consumed remains constant across all population densities of the prey. Holling (1966) derived a functional relationship which initially increases steeply, but the maximum rate of predation is limited by handling time ($k = 1/h$; Fig. 5.5). This Type II functional response applies to many invertebrate predators. However, as prey density increases, the proportion of the prey population consumed continually decreases so that the prey population is not limited by the predator.

Finally, the Type III functional-response curve is sigmoid with a very low rate of predation when population density of a particular prey species is low, but rate of predation increases very steeply as population density of prey increases before reaching a maximum rate of consumption (Fig. 5.5). A Type III response is typical of vertebrates that decrease pursuit time when prey are very rare, learn searching strategies as population density of prey increases, and switch among prey species in multi-species systems. For example, Sand et al. (2016) reported that roe deer (*Capreolus capreolus*) were more likely to be selected as prey items by gray wolves when roe deer populations were high, but gray wolves switched to moose (*Alces alces*), which have a higher caloric reward/kill, when roe deer populations were low. Both Type II (e.g., Canada lynx [O'Donoghue et al. 1998], coyote [Bartel and Knowlton 2005]) and Type III (e.g., Arctic fox [*Vulpes lagopus*], short-tailed weasel [*Mustela erminea*]; Gilg et al. 2006)

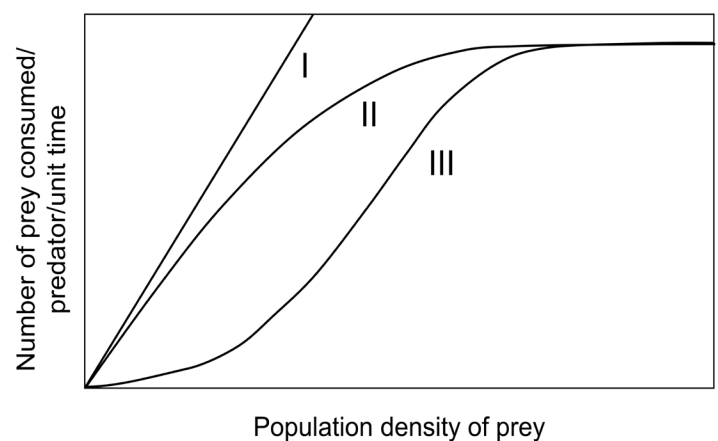


Fig. 5.5. Three hypothetical types of functional responses of prey consumption (proportion of prey population) per unit time by predators at a range of population densities of prey. Figure based on Gotelli (2009).

functional responses have fit the dynamics of furbearing species. A particularly important point regarding the sigmoid Type III response is that increasing rates of predation at lower population densities of prey results in population regulation of prey, but the total impact of predation peaks at intermediate density of prey, and then declines, enabling prey populations to escape from the regulatory effects of predation (Fig. 5.5).

Eventually, even the simple 2-species models incorporated greater ecological realism, including density dependence in both predator and prey populations, relatively efficient versus inefficient predators, aggregation of prey and predator, and refuges secure from predation. Regarding refuge from predation, observations and experiments (Brown et al. 1999) revealed that habitat selection by prey is often based on perceived risk of predation, which in turn alters the foraging strategy of predators, thus giving rise to the need to incorporate spatial distinctions into models (i.e., the influence of the landscape of fear; Bleicher 2017).

Widely cited studies in Yellowstone National Park, USA, describe the effects of the landscape of fear on how relationships between vegetation communities and elk (*Cervus canadensis*) were altered by the reintroduction of gray wolves (Laundré et al. 2001). DeWitt et al. (2019) used long-term data on predation by fishers (*Pekania pennanti*) on North American porcupines (*Erethizon dorsatum*) to quantify prey dynamics and fitness. Though the spatial characteristics of habitat and predation risk have been quantified as continuous landscape variables (Bleicher 2017), most population models still incorporate spatial variation in predation risk as binary distinctions between safe or vulnerable locations. Modifying simple models with many of these aspects of added realism reveal predator-prey dynamics that not only include neutral oscillations, but also damped oscillations, exaggerated oscillations leading to extinctions, and even stable equilibria (Rockwood (2006:227–231).

Simple 2-species models have also been applied to vegetation-herbivore interactions to reveal potential dynamics (Rockwood 2006). Surprisingly, population models for herbivores have not been specifically applied to furbearer systems, such as muskrats in marshes, although observations in those systems have had an important influence on understanding furbearer ecology. During the Marsh Ecology Research Program, Clark (2000) reviewed the literature on eat-outs (i.e., complete removal of vegetation due to foraging activities of muskrats), calculated the impact of muskrats on above-ground and below-ground vegetation resources, and assessed the influence of declines of available vegetation on muskrat survival. He concluded that declines in vegetation relative to flooding treatments, and the changes in demographic rates of muskrats, demonstrated that the latter responded to habitat changes rather than were the principal cause of it; i.e., the response was more bottom-up than top-down (Pace et al 1999).

As we noted since the beginning of this chapter, the study of predators, multiple species of prey, and the habitats on which they depend, has occurred in boreal ecosystems since the beginning of ecology. Somewhat in contrast to the bottom-up effects described above, studies of hares, voles (e.g., *Microtus* spp.), and predators in Scandinavia (Lindstrom et al. 1994), and snowshoe hares, Canada lynx, coyotes, and other predators in Canada (Krebs et al. 2001),

often included conclusions that top-down control by predators was the principal influence on ecosystem dynamics (Stenseth et al. 1997). The reintroduction of gray wolves to Yellowstone National Park is an often-cited example of the restoration of top-down effects of large predators, directly or indirectly affecting woody plants, populations of coyotes, red foxes, North American beavers (*Castor canadensis*), and elk and other large ungulates (Ripple and Beschta 2012).

Perhaps it should not be surprising that there is evidence collected from a variety of ecosystems that it is often a combination of top-down and bottom-up reciprocal effects that influence predators and prey. In the detailed analyses of the boreal ecosystem (Krebs et al. 2001), although hares died primarily from predation rather than malnutrition, when hares were at peak population densities, they impacted vegetation such that the quality of food available was less, thus revealing important bottom-up effects. Similarly, broad changes in bottom-up productivity across the landscape in Scandinavia determined the strength of the top-down effects after extirpation of Eurasian lynx (*Lynx lynx*) and gray wolves apparently resulted in the release of a mesopredator, the red fox (Elmhagen and Rushton 2007).

For completeness, it is important to mention that ecologists also developed simple 2-species models for competition as well as predation (Lotka 1925, Voterra 1926, Gause 1934). Almost all of the theory is based on simple organisms and is generally difficult to apply to animals such as furbearers. Broad reviews of the literature generally conclude that competition has intermediate effects on carnivores (Rockwood 2006). There are examples of results for furbearers predicted by simple 2-species models, such as niche compression in American martens (*Martes americana*) and fishers when reintroduced into suboptimal habitat (Manlick et al. 2017). The widespread extirpation of top-level carnivores such as gray wolves in North America (Prugh et al. 2009, Boyd et al. 2023 [Chapter 32]), and the accompanying increase of distribution and population density of coyotes (Ripple et al. 2013), is often cited as evidence of the competition among carnivores. After studies of the effects of coyote removal on predation by smaller carnivores on birds, Rogers and Caro (1998) hypothesized a mesopredator release, which others have recognized as founded in the combination of interference competition and predation (Elmhagen and Rushton 2007, Ritchie and Johnson 2009). It is worth noting the concerns expressed by Gehrt and Clark (2003) that mesopredator effects on abundant, widespread furbearing species (e.g., northern raccoons) has been overstated, and that direct, competitive effects are too simplistic to guide management of complex communities of predators.

The mesopredator-release concept has had many implications for furbearer management, particularly for species of conservation concern. For example, predation by coyotes on kit foxes (*Vulpes macrotis*; White and Garrott 1999) and swift foxes (*Vulpes velox*; Kamler et al. 2003) has complicated the conservation of these species. For some reason, competition and intraguild predation by coyotes seems to have suppressed population abundance of gray foxes (*Urocyon cinereoargenteus*) more than that of bobcats (Fedriani et al. 2000). Perhaps there are differences in

bottom-up effects of prey availability and habitat use that generate longer, unexplained fluctuations within these communities of mesopredators (Kamler et al. 2003).

Another application of top-down and competitive effects has been the use as justification for population control of mesopredators to enhance game-bird populations (Garrettson and Rohwer 2001), for population control of coyotes to decrease the number of livestock depredations (Knowlton et al. 1999), and population control of bears and gray wolves to decrease predation levels on caribou (*Rangifer tarandus*) and moose (Schwartz et al. 2003, Hebblewhite 2007). However, recognition by managers of ecosystem diversity and some level of public opposition to predator control based on social values (e.g., Hiller et al. 2021a) is making such management decisions increasingly complicated.

HARVEST OF FURBEARER POPULATIONS

Naïve intuition often leads to the viewpoint that removing animals by harvest will reduce population size, but experience shows that combinations of density-independent and density-dependent factors render such an outcome overly simplistic. Much of the traditional understanding of the effects of harvest on population size was developed based on models of logistic growth, especially as applied in management of fisheries, but also applied to marine mammals, ungulates, and some other species of large mammals. Visualize an unexploited population growing toward carrying capacity and described by a difference-equation logistic model. Then, if H_t individuals are removed after the birth pulse, the harvest rate is $h_t = H_t/N_t$, and the population remains unchanged as long as h_t exactly balances population growth rate, i.e.,

$$h_t = \left(\frac{\Delta N}{\Delta t} \right) = r_{max} \left(1 - \frac{N_t}{K} \right). \quad (14)$$

For a population with linear density dependence, the maximum rate of growth is reached at population size $N^* = K/2$ (Fig. 5.2), which can be harvested at a maximum rate of $h^* = r_{max}/2$, yielding a maximum sustainable yield (MSY) = $r_{max} \times K/4$ (Williams et al. 2002, Rockwood 2006). Note that it is possible to estimate h^* with an estimate of r_{max} (e.g., from trend data or an exponential model), but that estimating MSY requires estimates of both r_{max} and equilibrium population size (K). Assuming linear density dependence and using data from a muskrat population with $r = 1.05$ and $K = 2,500$, we estimated $h^* = 0.53$ maximum sustainable harvest rate, and $MSY = 656$ at $0.5K$. Clark and Fritzell (1992) found reported values for muskrats in the range of $h^* = 0.64 - 0.75$. A simulated population of muskrats with non-linear density dependence ($\theta = 0.3$) fluctuates substantially, but using $h^* = 0.70$, we estimated $MSY = 1,750$ at about $0.4K$.

The common-sense view of harvest effects on populations is really based on the assumption that harvest mortality is simply added to natural mortality. However, considering a simple density-independent model helps to introduce more complex potential relationships between natural mortality (m_0) and harvest mortality. If we define survival between surveys in a birth-pulse population,

with no harvest, as $S_0 = (1 - m_0)$, then only $S_0 \times N_t$ adults survive to reproduce and add young to the population:

$$N_{t+1} = bS_0N_t + S_0N_t. \quad (15)$$

Conversely, in a harvested population, total survival (S_t) might be directly reduced by harvest such that

$$S_t = S_0(1 - h_t). \quad (16)$$

The latter relationship treats the interaction between natural and harvest mortality as independent competing risks and is known as the additive mortality hypothesis (Williams et al. 2002). Ricker (1975) called this a Type I fishery, with natural and harvest mortality in distinct seasons and biologically unrelated to one another through density dependence. It is important to recognize that even with constant reproduction and natural mortality, applying h^* immediately after the birth pulse provides a larger sustained yield than a population harvested some months later, after natural mortality has reduced the standing crop (Caughley 1977:173–174).

The alternative extreme to additive mortality is that increase in harvest rate is exactly compensated by density-dependent decrease in natural mortality sources so that S_0 remains constant across all levels of h_t . Errington (1946) described the interaction of predation and other sources of natural mortality in this completely compensatory fashion and he extended the idea to predict the effects of harvest on muskrat populations (Errington 1963). Anderson and Burnham (1976) recognized that this completely compensatory mechanism is an ideal extreme expectation, and they introduced the concept of compensatory to a threshold level, h_c , of h_t (Fig. 5.6). Because compensation operates through the density-dependent

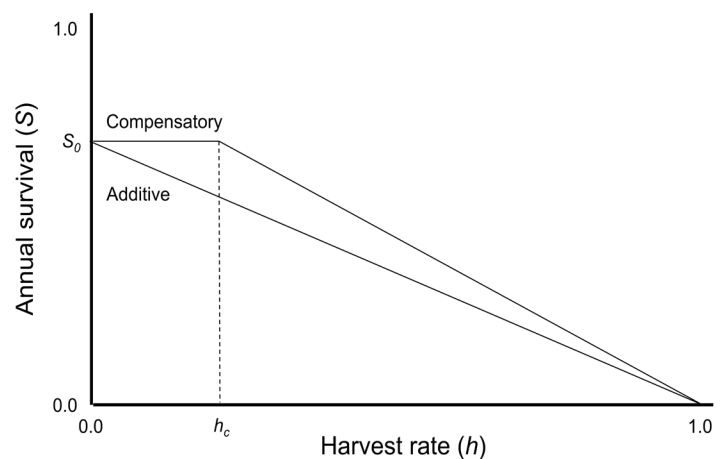


Fig. 5.6. Comparison of realized annual survival rates under a range of harvest rates and alternative assumptions of compensatory or additive harvest mortality. S_0 is annual survival in the absence of harvest. The threshold, h_c , is the point at which harvest becomes additive under the compensatory harvest mortality model. Figure based on Anderson and Burnham (1976).

reduction in natural mortality as harvest rate increases, the maximum h_C cannot exceed m_0 . So, for short-lived furbearing species (e.g., muskrats) with high m_0 , there is great capacity for compensation and high h_C . In contrast, for long-lived furbearing species (e.g., wolverines) with low m_0 , h_C is low, and the additive relationship among mortality sources applies over a wide range of harvest rates, suggesting a conservative harvest management strategy (Clark and Fritzell 1992, Banci and Proulx 1999).

It is important to recognize that the discussion above relates only to hypotheses regarding compensation among mortality rates. Population growth rate is also determined by reproductive rate, which has also been observed to be density dependent across the spectrum of furbearing species (Todd and Keith 1983, Clark et al. 1989, Clark and Fritzell 1992, O'Donoghue et al. 1997, McLeod and Saunders 2001). Furthermore, resilience to harvest depends not only on density-dependent relationships among reproductive and mortality rates, but also is related to social structure and spatial distribution of the population on the landscape (Banci and Proulx 1999).

Age Structure

Because many furbearing species are relatively long-lived, another complication of determining sustainable harvest rate is the age (or size) structure (Ricker 1975, Downing 1980). As we noted above, in a constant environment, λ depends on m (or F) and S , and ultimately the population reaches a stable-age distribution. If S is scaled, for example, by equivalent harvest rate of 25% of all age classes, the stable-age distribution remains unchanged, but λ is reduced (assuming that m remains constant). A practical implication is that simply observing a relatively constant age structure is not predictive of the potential for population growth. Furthermore, fluctuating environmental conditions and density-dependent responses in both m and S ensure that such constancy is unlikely anyway.

It is possible to incorporate harvest mortality into projection matrices and thereby consider alternative harvest strategies. This approach is conceptually appealing, but,

$$A = \begin{bmatrix} S_0(1-h_0)m_1 & S_1(1-h_1)m_2 & S_2(1-h_2)m_3 & S(1-h)m_3 \\ S_0(1-h_0) & 0 & 0 & 0 \\ 0 & S_1(1-h_1) & 0 & 0 \\ 0 & 0 & S_2(1-h_2) & S(1-h) \end{bmatrix} \quad (17)$$

requires an estimate of $h_{t(i)} = H_{t(i)}/N_{t(i)}$, i.e., the age-specific harvest rate. Also, note that Equation 17 could be extended to specify a functional relationship between S_0 and h (i.e., additive, compensatory, or threshold). Analytical sensitivity and elasticity analyses could be performed on the lower-level parameters of the functional relationship (as outlined above), although in practice a researcher might simply simulate various combinations of age-specific harvests as example scenarios. It is unlikely that $h_{t(i)}$ would be the same for all ages, with younger age classes more vulnerable to harvest than older classes. Theoretically, if a

population has reached a stable-age distribution and λ is known, then reproduction can be determined based on age-specific harvests (Williams et al. 2002:154). These properties are the basis of statistical population reconstruction (Fieberg et al. 2010).

As an example, we summarize the application of projection matrix analyses of Gosselink et al. (2011) to estimate sustainable harvest rates of bobcats in Iowa. They conservatively assumed that mortality from harvest would be additive and that the age structure reflected all sources of mortality, including sources such as incidental harvest, predation, and vehicle strikes. They assumed that a goal of maximum sustainable harvest rate would be harvest that reduces a population that is growing with $\lambda > 1$ to $\lambda = 0$ after harvest ($h^* = 1 - 1/\lambda$; Caughley 1977). They estimated mean $h \approx 8\%$, with an upper 95% confidence interval of $h \approx 16\%$. Both of these harvest levels are less than estimates that have been used by state wildlife management agencies for setting regulations (Crowe 1975, Knick 1990) and sometimes reported by state agencies to U.S. Fish and Wildlife Service to meet requirements of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; CITES 2023).

Banci and Proulx (1999) summarized the range of sustainable harvest rates of furbearers in Canada based on life-history characteristics, including range and distribution, reproductive rate, and habitat conditions. They characterized species such as sea otters and wolverines to have limited resilience and suggested sustainable harvest rates of $< 10\%$. They also described a variety of furbearing species (e.g., American marten, American mink [*Neovison vison*], American red squirrel [*Tamiasciurus hudsonicus*], North American beaver, North American river otter [*Lontra canadensis*], northern raccoon) as intermediate, with sustainable harvest rates ranging from 10 to 50%. Surprisingly, they suggested that Arctic foxes, coyotes, and red foxes could sustain annual rates of harvest in the range of 50–75%, a range similar to the highly resilient muskrat.

CONCLUSIONS

Although the models of density-independent and density-dependent growth are basic, they are useful to biologists as a framework for more detailed models and as a starting point for making informed management decisions. To this point, modeling harvest management has largely considered a single species at a time, usually focused on the goal of sustained yields. Increasingly, the extensions of these models have been used in conservation of rare and endangered populations. Too often, wildlife ecologists and managers have fixated on the mean (i.e., increasing or decreasing the standing crop) without knowledge of the variance. As we suggest in our chapter, incorporation of variation is increasingly practiced in modeling and management. Furthermore, models that incorporate overcompensation and undercompensation and the influence of time lags help biologists to predict that management decisions, such as changes in harvest regulations, may actually induce population fluctuations rather than dampen them (Fryxell et al. 2010). Matrix models are often useful because they readily enable biologists to organize population parameters of long-lived furbearing species.

Although biologists recognize the importance of multi-species top-down and bottom-up relationships, modeling of such complex systems for harvest management or conservation efforts has lagged (e.g., Hiller et al. 2018). For example, the expansion of mesopredator populations, and even geographic ranges of large predators in the face of low levels of natural mortality or decline in hunting and trapping effort, has resulted in proposals to harvest species (e.g., bobcat, mountain lion) in jurisdictions where harvest had not been allowed for decades. This transition has created social and political controversy, and the decision process is thus complicated beyond the traditional considerations of biological information (e.g., Hiller et al. 2021b, 2023 [Chapter 10]), such as predictions from population models presented here. Management options such as trapping for some furbearers is increasingly constrained because of societal pressure (Minnis 1998, Vantassel et al. 2010, Hiller et al. 2021a). The use of population models to provide stakeholders with possible outcomes of harvest scenarios is a critical component to reducing at least some of the controversy surrounding these species (Chase et al. 2000). Given that export of pelts and products of many furbearing species or subpopulations (e.g., bobcats, North American river otters) are also regulated through international treaty (i.e., CITES 2023, Batcheller and Organ 2024 [Chapter 3]), the application of appropriate population analyses and stakeholder views have international importance.

The expansion of the human population and the concurrent increase in demand for agricultural and energy production is causing habitat loss or destruction throughout North America. Fragmentation in boreal forests and losses of remaining grassland ecosystems is impacting once common species and further isolating species of conservation concern (Lewis and Weir 2024 [Chapter 8]), such as American martens (Fortin and Cantin 2005, Gehring et al. 2019), swift foxes (Alexander et al. 2016), and wolverines (Ruggiero et al. 2007). Spatial models are increasingly applied to understand the consequences of habitat loss and fragmentation, plan the establishment of corridors (Benson et al. 2019), and understand the likelihood of success when species such as black-footed ferrets (*Mustela nigripes*) are translocated (Jachowski et al. 2008). Conversely, some furbearing species (e.g., coyotes, northern raccoons, striped skunks [*Mephitis mephitis*]) are readily adapting to urban environments and their presence is becoming a new challenge for state wildlife management agencies (Gehrt et al. 2011, Sálek et al. 2015). Both traditional and spatially explicit models are being applied to compare management alternatives.

Finally, climate change is altering plant and animal distributions on a global scale. Climate change may affect the type of vegetation available at public-land areas, such as national parks and national wildlife refuges, and population models can help managers predict what will happen as breeding habitat becomes unsuitable for species limited to isolated patches of habitat (Licht et al. 2017). Even at large spatial scales such as extensive boreal forests, climate and associated large-scale changes are having effects on furbearers (Marcot et al. 2015). Multi-species modeling of furbearer communities could be especially useful in assessing the impacts of habitat losses to agriculture and energy development.

The origin of the word conservation is from Latin for conservative. In some sense, the earliest population modeling largely ignored variation and managers tended to strive for the status quo in their decision making. Modern conservationists work in a world context of considerable ecological and environmental variation (Lewis and Weir 2024 [Chapter 8]), much of which impacts furbearer populations over the long term, but is often out of their control. In the above context, the principles of population ecology are a fundamental starting point, more recent theory advances those principles, and biologists now have a toolbox of applications that they can use for managing and conserving furbearers.

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