Design and Analysis of a Population Model for Beaver (*Castor canadensis*)

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Abstract

A mathematical model for the dynamics of a harvested population of beaver (*Castor canadensis*) was developed based on the natural history and biochronology of the species. This discrete-time, deterministic model breaks the annual cycle of a beaver population into six periods and tracks the transitions between periods for forty sex/age classes. Density-dependent effects are incorporated in breeding rates of the young age classes and in dispersal mortality rates. General results from simulations with the model qualitatively matched results from several observational studies. Specific results from the model, however, included phenomena that have not yet been studied in the field: (1) the average colony size was an increasing function of occupancy rate (a measure of colony density); (2) an early harvest (prior to breeding) caused a greater reduction in the growth rate of the population than a late harvest when the population density was low, but the pattern was reversed at high population density; and (3) the occupancy rate remained near 1.0 (all potential colony sites filled) for sustained harvest rates below about 20%, and decreased sharply with increases in harvest rate above that threshold. In the range of occupancy rates typically sought through management, the population size and occupancy rate were very sensitive to harvest rate, suggesting that there is considerable potential to control population size through adjustment of the harvest. Sensitivity analysis was used to identify priorities for parameter estimation in this model. A single parameter, the base adult litter size, was identified as the most important determinant of population growth rate, and hence, the parameter that should be most carefully estimated. The dynamics of this model depended heavily on the way density-dependent dispersal mortality was expressed, thus providing motivation for specific field studies to confirm or refute the predictions obtained through simulation.

Keywords: Beaver, *Castor canadensis*, structured population model, density-dependence, growth rate, sensitivity analysis, parameter estimation, simulation.

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1 Introduction

In this paper I develop and explore a comprehensive population model for beaver (*Castor canadensis*) based on the biology of the species. There are four major purposes in building such a model. First, I endeavor to *synthesize* existing knowledge about beaver biology so that it can be examined holistically. Such a synthesis can shed light on population dynamics, test long-held assumptions, and expose inconsistencies or gaps in current knowledge. Second, this model can be used to *generate* hypotheses to help guide field studies. Third, this model can help *prioritize* parameter estimation needed for management purposes by identifying those parameters whose uncertainty has the greatest effect on population dynamics of interest. Ultimately, this prioritization can also be used to guide refinement of the model itself, in an effort to produce a model that is useful to managers and that captures the key dynamics. Fourth, this model can be used as a *simulation device* for testing management policies. By using the detailed population model to represent the "truth" of nature, Runge (1999) examined the effects on management outcomes of having only partial knowledge of the truth and of making major changes to the way management is carried out. In this paper, I examine previous beaver population modeling efforts, develop a model based on biological information in the literature, then conduct several simulation experiments with the model to explore its dynamics.

The model developed is a single-species, discrete-time, deterministic population model (though provisions are made to incorporate environmental stochasticity). Males and females are distributed among twenty age classes, the life span of beaver. The sex/age class is the basic unit in the model, but colony structure is incorporated to some extent.

This paper was extracted from Chapter 3 of Runge (1999) with some minor modifications. I gratefully acknowledge the help of Aaron N. Moen, Charles E. McCulloch, Deborah H. Streeter, and Robert F. Gotie in the development of this work.

2 Previous Efforts to Model Beaver Populations

Surprisingly, for a species that has been studied so heavily, very few attempts at beaver population modeling have been published in the peer-reviewed literature. There is really only *one* full-fledged population model for beaver (Molini et al. 1981). There certainly must be quite a number of population models of varying complexity in use by beaver managers, and accounts of these may be found in internal documents, but any knowledge of them is not widely available. In addition, there are references to several theses and dissertations that contain information on population dynamics, but much of this work was never published. There is, however, a tremendous amount of information about particular aspects of population dynamics (see review in Runge 1999), information that needs to be synthesized into a flexible, and biologically relevant, population model for beaver.

2.1 Life tables and related calculations

The most basic information about population dynamics is not so much a model but a description of a population. For instance, calculation of survival and fecundity rates in a life table *describes* a population, but it takes an additional logical step to assemble a model from this. There are a number of studies that provide some fairly complete descriptions of beaver populations. Payne (1984a, 1984b) presents relative mortality and fecundity estimates for beaver in Newfoundland, breaking the population into age-classes, but not differentiating between the sexes. These data are certainly extensive, but as pointed out by Lancia and Bishir (1985), Payne (1984a) makes some serious inferential errors. Nevertheless, with a little effort, and a few assumptions less radical than Payne's, a Leslie matrix model could be constructed from this information.

Novak (1977, 1987a) and Swenson et al. (1983) provide formulas for estimating the average colony size from age-specific harvest data. Though this concerns population *estimation*, we might begin to think of these calculations as *models* because of some assumptions about how the colonies are structured. Specifically, they rely on the fact that a colony contains at most two reproductively mature adult beaver, and use this fact to convert the proportion of adults in the harvest into an estimate of the average colony size. Though this alone does not make such a calculation a population model, it hints at an approach that is used in some population models for beaver (e.g., Molini et al. 1981). This example, and the one before it, are characteristic of many studies of population dynamics of beaver which stop short of assembling their results into population models.

2.2 Logistic models

A number of studies have suggested that beaver productivity is density-dependent (Pearson 1960, Gunson 1970, Payne 1984b), so it is natural that a number of authors have mentioned a logistic model as appropriate for beaver (Nash 1951, Lancia and Bishir

1985, Baht et al. 1993). Lancia and Bishir (1985) fit a logistic model to their data from a nonexploited population from Prescott Peninsula, Massachusetts, and argued that the intrinsic rate of increase should be between 0.35 and 0.45 for most beaver populations. They were using this model as an example to illustrate their points in an argument about something else, however, and did not seem to intend that such a simplistic and empirical model be taken too seriously. Nevertheless, Baht et al. (1983) took them at face value and used a logistic model (with Lancia and Bishir's point estimate for the rate of increase) in the analysis of a beaver management problem.

2.3 Colony models

In an unpublished model used internally in the New York State Department of Environmental Conservation (NYSDEC), Robert F. Gotie (pers. com.) took a very different approach to modeling a beaver population. Responding to studies that suggested that beaver population growth depends on colony occupation rates (e.g., Parsons and Brown 1979), Gotie built a model with the colony, rather than the individual, as the central unit of the population. Instead of having a structured population with individuals divided into age-classes, Gotie's model has a structured population with colonies divided into single, pair, or family classes. Transitions between these classes take the place of mortality and fecundity—for instance, two single colonies can merge to become a pair colony (through mating), a pair colony can become a family colony (through reproduction), a family colony can produce a single colony while remaining a family colony (through dispersal of two-year-olds), etc. Most of Gotie's estimates of these class transitions are based on only one study (Payne 1982) and would need more justification and support to be convincing. Nevertheless, this model offers the important reminder that beaver life-history depends critically on the colony.

Gotie's model can be described as a matrix model, with the state of the system being the number of colonies in each of the three classes, and a 3 x 3 transition matrix being used to calculate the state of the system in the next time period. By treating the transition rates as transition *probabilities*, this could be converted into a Markov model. To be more realistic, however, I would increase the number of possible classes to include a much finer structure to the population. For instance, I would have several "single" classes: single yearling male, single yearling female, single adult male, single adult female. The "family" classes would be fairly complex, distinguished by the age and sex composition of the colony. The transitions would then look, for instance, at the probability of 2-breeding-adult, 2-yearling, 4-kit colony becoming a 2 breeding-adult, 2-yearling colony (through dispersal or death of the yearlings and 50% survival of the kits). In essence, this would turn into an individual-based model, with the status of the individual's colony being a key consideration in determining the probability of survival or reproduction. Estimation of some of the transition probabilities would be almost sheer speculation, and there would be a great many to estimate. Thus, while such a model might be of interest on theoretical grounds, I would not pursue it for practical purposes.

2.4 Stochastic models

The most sophisticated and carefully considered beaver population model available in the published literature is that of Molini et al. (1981). This model, which was designed to represent a nonexploited, growing population, incorporates demographic stochasticity and density-dependence in an age-structured depiction of the female segment of the population. Demographic stochasticity is included in five life-history events: survival, dispersal, and pair formation are all modeled with binomial distributions; replacement of deceased females in established colonies with subadult females is modeled with a combinatoric box-and-ball type of distribution; and litter size is modeled with an empirical distribution. The binomial probabilities used for the dispersal rate and the pair formation rate are both density-dependent. Dispersal is assumed to be a decreasing function of density—as density increases and fewer uncolonized sites are available, two-year-olds reduce their risks by delaying dispersal. The pair formation rate among dispersed sub-adults also depends on the availability of uncolonized sites. As the density increases and fewer sites are available, dispersed beaver are unable to form a pair and establish a colony, and are assumed to die. At saturation densities, most of the mortality in the population is of these dispersed sub-adults that failed to form a pair. All other survival rates are quite high (> 95%). Thus, the major limiting resource in this model is the number of potential colony sites, and the model shows sigmoid growth. If the model were expanded to include harvesting, so the density could be artificially maintained at a low occupancy rate, this effect of extremely high mortality of sub-adults would be substantially reduced. A final component of interest in this model is the mortality of all kits and yearlings in a colony in which the adult females dies and is not replaced by a sub-adult.

Simulations with this model produced results that roughly resembled the observed population trajectory in Prescott Peninsula, Massachusetts (Molini et al. 1981). In addition, the equilibrium age-distribution and age-specific survival rates were supported by other observations in the literature, although sub-adult mortality seemed to be higher than typically reported. The simulations showed considerable variation as a result of the demographic stochasticity, although Molini et al. did not look at how this variation was affected by the maximum number of colony sites (50 in their simulations). I would expect that this variation would be less significant across larger areas where the maximum colony number, and hence, population size, was much higher. It is not clear how relevant the two major forces of this model, density-dependence and demographic stochasticity, would be to the manager of a large, exploited population that was held far below the saturation level.

3 Population Model

I have taken components of the aforementioned models and combined them with other insights about beaver population dynamics from the literature to develop a comprehensive, biologically-based population model. The context underlying this model is a large, managed beaver population that is actively trapped and maintained at a density below any natural saturation level ("carrying capacity").

The population model developed herein treats the sex/age class as the primary unit and tracks the dynamics of the population through 6 periods in each successive annual cycle. The population size in age class a and sex class s, during period p of year t is given by $x(a,s,t,p)$. Thus, the total population size during period p of year t is

$$\sum_a \sum_s x(a,s,t,p) . \qquad (1)$$

The computer code based on this model, used subsequently for simulation, can be found in the appendices of Runge (1999) or obtained from the author in electronic form.

3.1 Biochronology

The concept of biochronology, introduced by Moen (1973), refers to the sequence of significant events that occur in the life of an individual organism. The model is structured around the natural biochronology of beaver, shown schematically in Figure 1. The annual cycle begins with the *post-parturition population*, the population immediately following the birth of kits. In the northeast United States, this occurs in early June (Jenkins and Busher 1979). The population suffers natural mortality through the summer and early fall as a result of a number of factors, including dispersal and predation, and in kits, malnourishment, to produce the *post-dispersal population*. By this point in the annual cycle, most dispersal is complete and the beavers begin to prepare for winter. Over the next 8 months, the population undergoes natural mortality due to a number of factors, collectively called "winter mortality," including starvation, exposure to the elements, and predation, to produce the *pre-parturition population*. At this point, all living individuals are promoted to the next age class, and kits are born to produce the *post-parturition population*, and the cycle begins again.

Human intervention in this biochronology, that is, wildlife management, adds two additional forms of mortality and inserts one monitoring event per annual cycle, as shown in the schematic in Figure 2. The two forms of mortality are nuisance control and regulated fur harvest, the latter divided into an early and a late season. The monitoring, when practiced, usually occurs after leaf fall and before freeze-up (Hay 1958), and typically consists of aerial surveys. As before, the annual cycle begins with the *post-parturition population* (period 1, $p = 1$). Nuisance control from this point until the early harvest season (around October 1) removes animals to produce the *post-weaning population* ($p = 2$). This includes the death of kits as a result of the removal of their mother through nuisance control prior to weaning. Natural summer mortality acting during the next transition results in the *pre-harvest population* ($p = 3$, equivalent to the *post-dispersal population* in the absence of human intervention). Since aerial counts are usually made at this time, this population is also the population which is surveyed. Early harvest and nuisance control, acting throughout the late fall and early winter, produce the *post-early-harvest population* ($p = 4$). This population then undergoes natural winter mortality to become the *pre-late-harvest population* ($p = 5$). Late harvest and nuisance control, acting throughout the late winter and early spring, produce the *pre-parturition population* ($p = 6$). Living individuals are promoted and kits are born to produce the *post-parturition population* ($p = 1$), and the cycle begins again.

Several details of the biochronology chosen for the population model require comment. First, the harvest is broken into two periods, early and late, to acknowledge that harvest is typically bimodal with peaks occurring during open water periods at the beginning and end of the season, and to reflect the

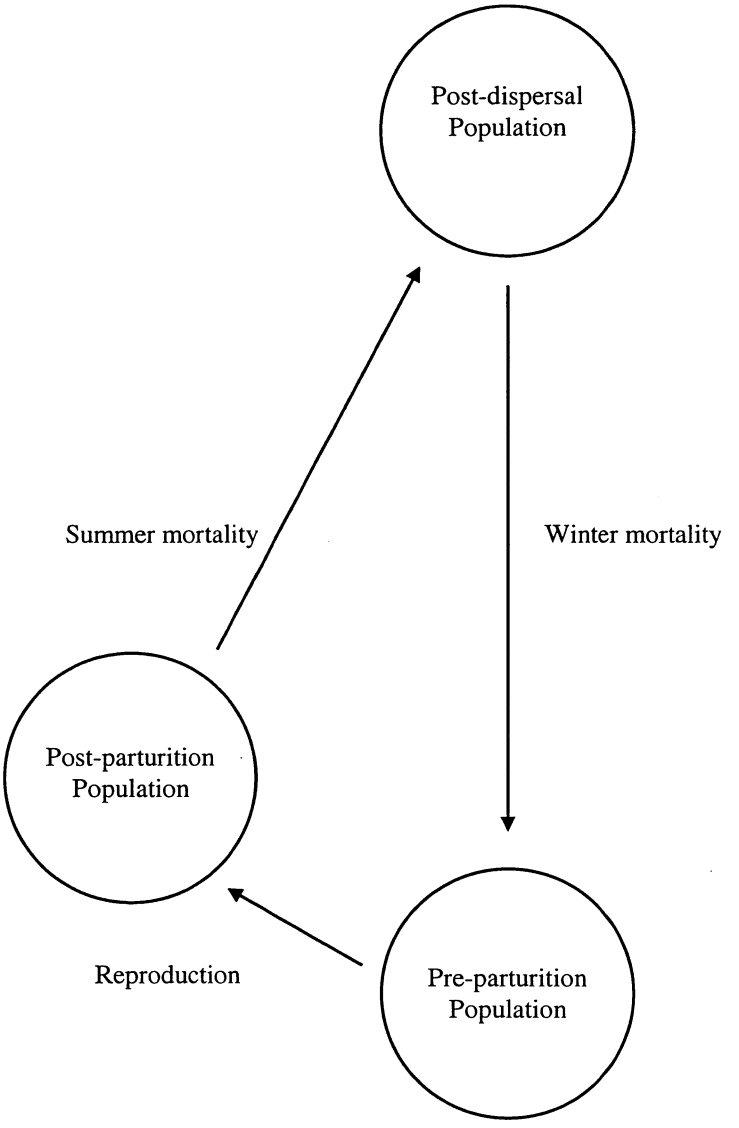

Figure 1. Biochronology of the beaver population model in the absence of human intervention. The circles represent the population at three periods within the annual cycle and the arrows represent the events which change the population. Compare to Figure 2.

management practice of extending the season or having a late season to add to a low early harvest. From a biological standpoint, it is important to distinguish these periods, since if the male of a pair is trapped, how that affects reproduction depends on whether the male was removed before or after breeding. Second, winter mortality is placed between these two periods during the time when the weather is coldest, the ice is thickest, and the risk of death due to exposure or lack of access to food is greatest. While natural mortality and harvest act simultaneously from late fall to early spring, the harvest tends to be lower during the coldest part of winter. It is reasonable to expect natural mortality rates due to cold, ice, and inability to reach a food cache to be highest at this time, and thus, modeling these factors as separate is not a great deviation from reality. Third, a similar separation of nuisance control and natural summer mortality is made in the model. Animals taken by nuisance control between parturition and the beginning of the trapping season are removed from the modeled population first, and the remaining individuals face natural mortality. While natural mortality and nuisance control actually act simultan-

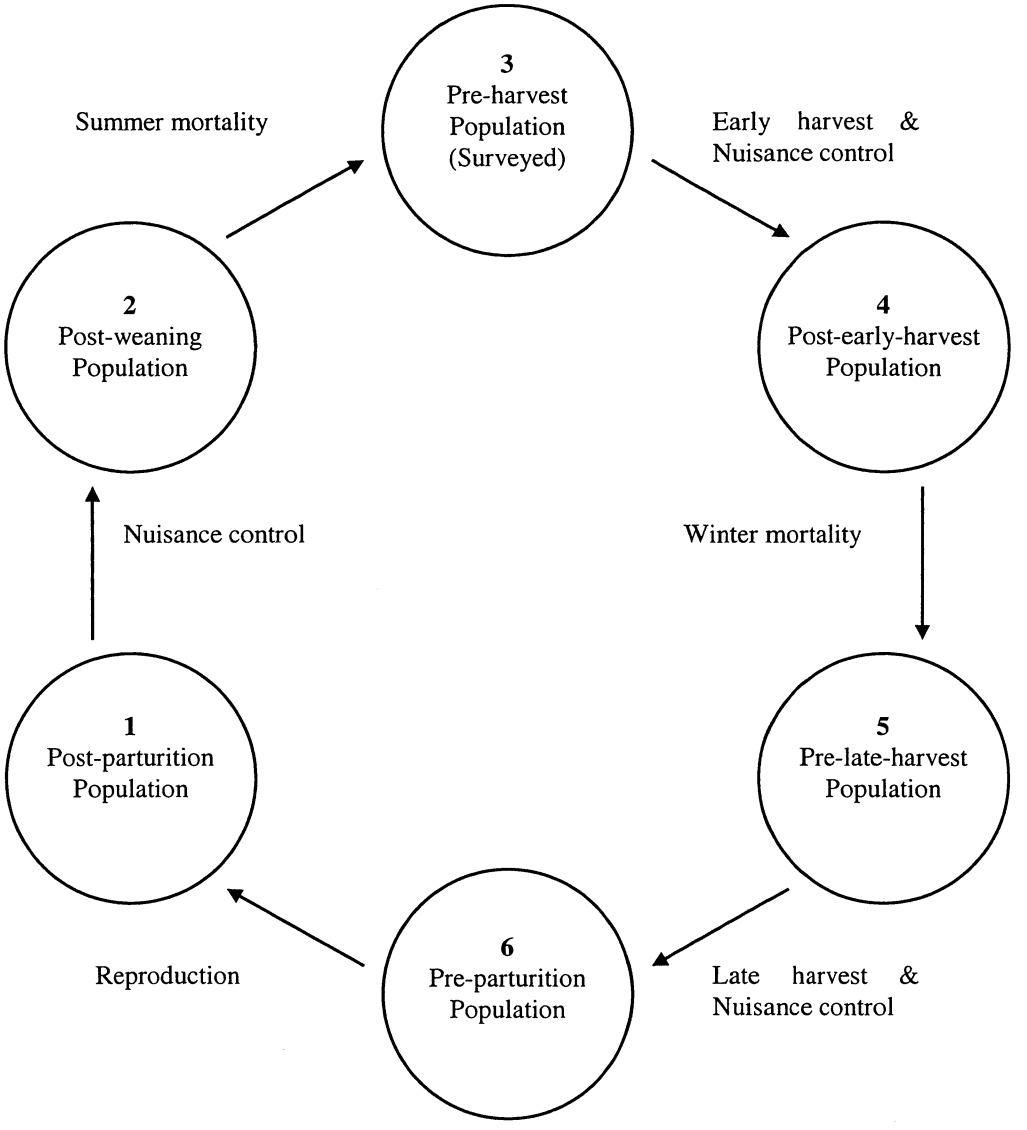

Figure 2. Biochronology of the beaver population model in the presence of human intervention. The circles represent the population at the six periods within the annual cycle and the arrows represent the events that change the population

eously, constructing the model this way reflects the fact that some of the animals that would have died from natural causes were already taken by nuisance control.

3.2 Population structure

This population model structures the beaver population into forty sex/age classes. The individuals in these classes are also grouped into colonies.

Age classes. Twenty age classes are used in the model, age 0 (kits), age 1 (yearlings), age 2 (two-year-olds), and ages 3-19 (adults). Kits are in age class 0 at birth and remain there until the following parturition period, when they advance to age class 1. All other age classes also advance at the time of parturition. Twenty age classes are used because each age class in the potential life span of an individual needs to be represented in order to capture the many age-related population dynamics.

Sex classes. Each of the twenty age classes is further divided into two sex classes, male and female. The number of male yearlings alive in period p of year t, for instance, is designated as $x(1, \mathrm{M}, t, p)$.

Colony structure. The population dynamics are modeled at the level of the sex/age class, and the

number of colonies is calculated from this for two reasons: first, the density dependence (see "Density dependence," p. 9) is governed by the fraction of potential colony sites that are occupied (the occupancy rate); and second, census methods for beavers typically count *colonies*, not individuals. The number of colonies is determined by summing the number of potentially breeding females in the pre-harvest population (period 3). Since females that are 1.5 years old (yearlings, age class 1) in the fall sometimes disperse and breed if the population density is low, their breeding rate needs to be taken into consideration, as does that of age class 2 females. Females in age class 3 and above are assumed to have dispersed and formed colonies. Thus,

$$b_1 x(1,F,t,3) + b_2 x(2,F,t,3) + \sum_{a=3}^{19} x(a,F,t,3) \quad (2)$$

gives the number of colonies in year t, where b_1 and b_2 are the breeding rates for yearling and two-year-old females in year t. These breeding rates are discussed in more detail below. Note that this method of calculating the number of colonies from the age structure assumes that two adult females are never found in the same colony and that a colony always contains a breeding female, assumptions that have been supported in field studies (Bergerud and Miller 1977).

3.3 Initialization

In an iterative model such as this, an initial sex/age structure needs to be specified as a starting point from which calculations can be made. For the model to be realistic, the initial population needs to be represented with a biologically reasonable population structure. Since the survey is usually taken of the pre-harvest population, the initial population is constructed for period 3 (p = 3). The structure of this initial population is controlled through five parameters: the total size of the population, the overall sex ratio, and the fraction of kits, yearlings and two-year-olds in the population. The fraction of adults in the population is found by subtraction. The total population is subdivided proportionally into male and female kits, yearlings, and two-year-olds. To initialize all of the adult age classes, it is not acceptable to divide the adults equally among all age classes. Rather, the adult age classes need to reflect the declining proportions due to mortality, based on an average total annual adult mortality rate (m, default 0.3). The adult age classes are then initialized so that the ratio of any age class to the previous age class is the survival rate ($1 - m$) corresponding to this mortality rate. This is done by noting that the numbers of adults in each age class form a geometric series with parameter ($1 - m$), and the total number of adults is a partial sum of this geometric series. Specifically, the number of adults is given by

$$\sum_{a=3}^{19} \sum_{s} x(a,s,t,3) \quad (3)$$

where

$$x(a+1,s,t,3) = (1-m) \cdot x(a,s,t,3) \ . \quad (4)$$

Equation 3 can thus be written as

$$\sum_{a=3}^{19} \sum_{s} x(3,s,t,3)(1-m)^{a-3} \ , \quad (5)$$

which is a partial geometric series that can be simplified to

$$\left[\sum_{s} x(3,s,t,3) \right] \left[\frac{1-(1-m)^{17}}{1-(1-m)} \right] . \quad (6)$$

Setting equation 6 equal to the known total number of adults and solving for the first sum results in the number of adults in age class 3. These are then divided between the two sexes. From there, equation 4 is used to calculate the number of adults in all other sex/age classes.

This initialization requires six parameters (total population size, fractions of kits, yearlings, and two-year-olds, fraction female, and average annual adult mortality). The population initialized in this manner will not necessarily match the sex/age class distribution of a real population or of one produced by the model after several iterations for three reasons: first, the same sex ratio is used across all age classes; second, all adults are assumed to be equally vulnerable, that is, have the same mortality rate; and third, the last five parameters may not be correct. Nevertheless, if the last five parameters are chosen carefully, the initialized population is expected to have a reasonable sex/age structure. Where needed, a more detailed initialization method repeats the following set of steps until a stable sex/age distribution is found: the population is initialized as above, run through the model for one time step, and reinitialized with the resulting age and sex distributions.

3.4 Early harvest and nuisance control

In this and following sections, the details of the steps of the model are described chronologically, beginning

with the *pre-harvest population*. As noted above, the population is initialized at the pre-harvest period (p = 3). The transition from the *pre-harvest population* (p = 3) to the *post-early-harvest population* (p = 4) is a result of the impacts of early harvest and nuisance control. In the northeast United States, this time period runs from around October to February. The model requires the specification of the known total harvest and the known total number of beaver removed by nuisance control.

Harvest. The total number of harvested animals is removed from the population using sex- and age-specific relative harvest rates, referred to herein as harvest vulnerabilities. Most studies have shown that harvest is not usually biased by sex (Payne 1982) or age (Novak 1987a), thus the default values for all the harvest vulnerabilities are 1, but the option is included in the model to specify other values.

Nuisance control. The beavers removed by nuisance control during this transition are removed from the modeled population proportionally across all sex/age classes. In nuisance control situations, whole *colonies* are typically removed. Provided that colonies removed are representative of all the colonies, colony composition should reflect population composition, and there should be no bias by sex or age in the beavers removed by nuisance control.

Parameters and equations. The model requires specification of the total number harvested, $H(t, 3)$, and the total number removed by nuisance control, $N(t, 3)$. The harvest vulnerabilities are given by $v_H(a, s, t)$, and represent relative rates of harvest between sex/age classes. The default value for all of these is 1. The harvest *rate* for a given sex/age class is

$$h(a,s,t,3) = \frac{v_H(a,s,t)H(t,3)}{\sum_{a,s} v_H(a,s,t)x(a,s,t,3)}. \qquad (7)$$

Since it is assumed there is no bias in the nuisance control, there is only one nuisance control *rate*,

$$n(t,3) = \frac{N(t,3)}{\sum_{a,s} x(a,s,t,3)}. \qquad (8)$$

The period 4 population is calculated, for all a and s, as

$$x(a,s,t,4) = x(a,s,t,3)\cdot(1 - h(a,s,t,3) - n(t,3)) \quad (9)$$

with adjustments made to be sure that the sum of the harvest and nuisance rates does not exceed 1.0 for any sex/age class.

3.5 Winter mortality

The transition from the *post-early-harvest population* (p = 4) to the *pre-late-harvest population* (p = 5) is a result of the impacts of winter mortality. As noted above, this transition reflects the fact that during the coldest part of the winter, when ice is thickest, the harvest rates drop and much of the mortality can be attributed to natural causes. In the northeast United States, this transition occurs from mid-January to late February. Mortality rates for male and female kits, yearlings, two-year-olds, three-year-olds, and adults need to be specified. In addition, vulnerability curves are used to represent the relative mortality in the female and male adult age classes.

Mortality. Mortality rates may differ between sexes and between age classes. In the kit, yearling, two-, and three-year-old age classes, the number that survive is the product of the initial number and the survival rate for that age class and sex.

Adult vulnerability. For adults, a vulnerability curve reflects the relative mortality in different age classes (Figure 3). This relative mortality is multiplied by the base mortality rate to determine the mortality rate for a particular adult sex/age class. Of course, if this product is greater than 1.0, the mortality is truncated to 1.0. The model allows for different vulnerability curves for each sex.

Parameters and equations. The model requires the winter mortality rates for male and female kits, $mw(0, M, t)$ and $mw(0, F, t)$, yearlings, $mw(1, M, t)$ and $mw(1, F, t)$, two- and three-year-olds (specified analogously), and adults, $mw_{AM}(t)$ and $mw_{AF}(t)$. Default values are shown in Table 1. In addition, vulnerability curves for male and female adults need to be constructed. Based on the age-specific mortality patterns of mammals in general, one might expect adult beaver vulnerability to rise slowly in the younger adults, then more sharply in the very old. Thus, the default vulnerability curve is modeled with a double exponential expression

$$v(a,s) = \frac{c_1(s)e^{-k_1(s)a} + c_2(s)e^{-k_2(s)a}}{c_1(s)e^{-4k_1(s)} + c_2(s)e^{-4k_2(s)}}, \qquad (10)$$

which gives a vulnerability of 1.0 to age class 4. Note that the specified base adult mortality rate is the mortality rate for an age class with a vulnerability of 1.0. The default values used for the parameters of this vulnerability curve are those found by fitting the curve to Payne's (1984a) data, and are the same for both sexes: $c_1 = 0.62$, $c_2 = 3.3 \times 10^{-8}$, $k_1 = 0.048$, and $k_2 = 0.95$. Because of the way the denominator of equation 10 adjusts the vulnerabilities, the actual values of c_1 and c_2 are not important, only their ratio.

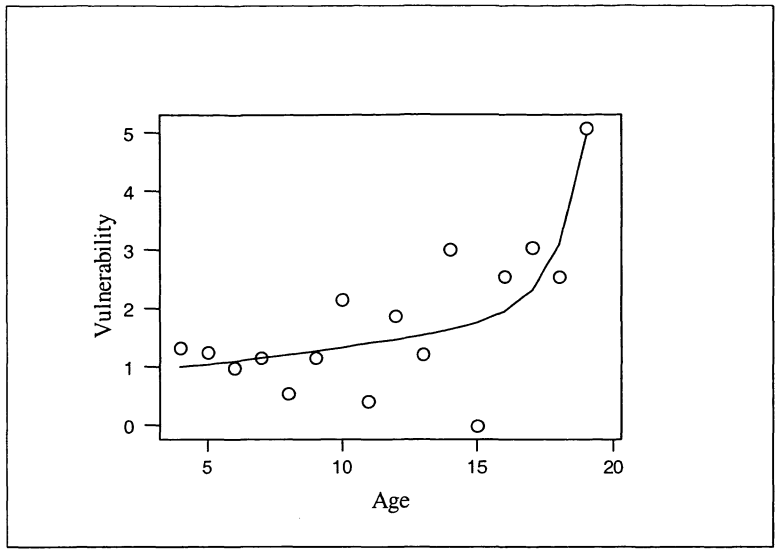

Figure 3. Adult vulnerability curve. The mortality rate for an age class is found by multiplying the base adult mortality rate by the vulnerability for that age class. The open circles are the age-specific mortality rates calculated by Payne (1984a), adjusted so the fitted line gives a vulnerability of 1 for age class 4. The fitted line was found by nonlinear least squares regression (using SAS PROC NLIN), using a double exponential function.

The period 5 population is calculated with

$$x(a,s,t,5) = x(a,s,t,4)\cdot(1-mw(a,s,t)) \quad (11)$$

for all s and for $a \leq 3$, and with

$$x(a,s,t,5) = x(a,s,t,4)\cdot(1-mw_{As}(t)\cdot v(a,s)) \quad (12)$$

for all s and for $a > 3$, subject to the constraint that

$$mw_{As}(t)\cdot v(a,s) \leq 1. \quad (13)$$

Table 1. Default winter mortality rates. The mortality rate for kits is based on a comparison of Svendsen (1980) and Gunson (1970), and that for yearlings is based on Svendsen (1980) and Molini et al. (1981). The default value used here is the average of the extremes reported by Boyce (1981, 20%, Alaska) and used by Molini et al. (1981, 0%, Massachusetts).

Sex\Age	0	1	2	3	Adult
Male	0.073	0.016	0.100	0.100	0.100
Female	0.073	0.016	0.100	0.100	0.100

3.6 Late harvest and nuisance control

The transition from the *pre-late-harvest population* (p = 5) to the *pre-parturition population* (p = 6) is a result of the impacts of late harvest and nuisance control. In the northeast United States, this transition runs from about March to June. The model requires specification of the known total harvest and the known total number of beaver removed by nuisance control. Note that the late harvest season (if it exists) only lasts until late March, but nuisance control can continue until the date of parturition.

The calculations for this transition are exactly analogous to those for the early harvest transition (see "Early harvest and nuisance control," page 6), and the same vulnerabilities are used. Letting $H(t, 5)$ and $N(t, 5)$ represent the total number of animals removed by harvest and nuisance control during this time period, the harvest and nuisance control *rates*, $h(a, s, t, 5)$ and $n(t, 5)$, are calculated with equations analogous to 7 and 8, respectively. Then, the period 6 population is calculated, for all a and s, as

$$x(a,s,t,4) = x(a,s,t,3)\cdot\left[1-h(a,s,t,3)-n(t,3)\right] \quad (14)$$

with adjustments made to be sure that the sum of the harvest and nuisance rates does not exceed 1.0 for any sex/age class.

3.7 Reproduction

The transition from the *pre-parturition population* ($p = 6$) to the *post-parturition population* ($p = 1$) is a result of all animals advancing in age class and of females giving birth. Unlike the other transitions in this model, this transition is treated as being instantaneous in time, thus assuming that all births occur at once. The following parameters are required: reproductive rates (in kits/litter) for yearlings and adults; the percentage of female kits in the litters; density-dependent relationships for the fractions of yearling, two-, and three-year-old females that breed; and a relative reproductive rate curve for adult females.

Density dependence. A density dependent effect on reproduction has been noted in several studies (Henry and Bookhout 1969, Nordstrom 1972, Kudrisahov 1975, Vanden Berge and Vohs 1977, Swenson et al. 1983, Peterson and Payne 1986, see review in Runge 1999). In particular, when the occupancy rate is low, sexual maturation occurs earlier (Parsons and Brown 1979, Payne 1982, 1984a). In the model, the user defines three density-dependence curves that relate the fractions of young females that breed to the occupancy rate (Figure 4). This curve assumes that there is a maximum fraction breeding up to a certain density, then a linear decline to a minimum fraction breeding. As there is no evidence for density-dependence in breeding or pregnancy rates in older age classes, the model assumes that all females four and older potentially breed.

Relative reproductive rates. Litter size in adult females increases with advancing age of the mother until about age 8, stays steady for a number of years, and then declines somewhat in the very old (Novak 1987a, Payne 1984b). The model allows specification of the relative reproductive rates of females by age class. This relative rate is multiplied by the base adult litter size to arrive at the average litter size for a particular age class of females. The default relative reproductive rate curve uses a quadratic relationship that closely matches data found in the literature (Payne 1984b, Gunson 1967). Note that this curve has a maximum of 1 for females giving birth at ages 8 and 9, thus, the base adult litter size should be the average litter size for females of such ages, not for all females.

Sex ratio at birth. The model assumes that the sex ratio at birth is not density dependent and is the same for all age classes of females. There is not convincing evidence in the literature that the female fraction in the litters is any different from 50%, which is the default value used in the model.

Effect of early harvest on breeding. The reduction of pregnancy rates due to trapping of the male after pair-bonding but before breeding (i.e.,

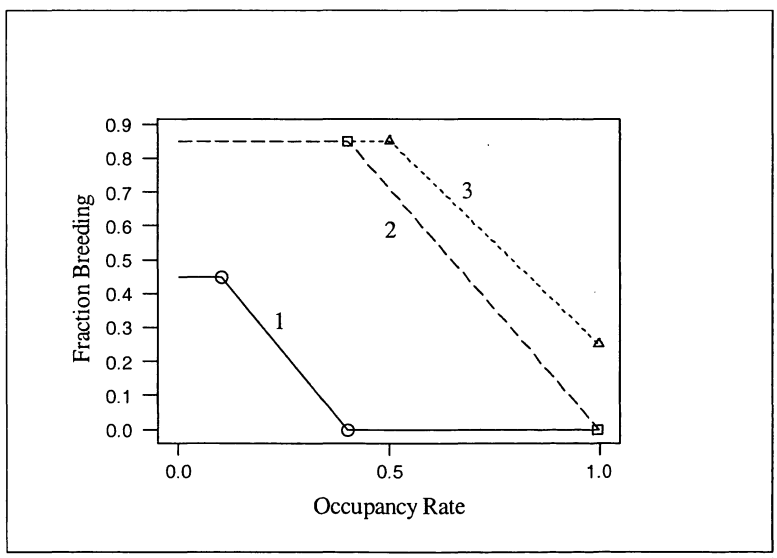

Figure 4. Density-dependence of reproduction in the younger age-classes. The fraction of females breeding is shown for yearlings, two-year-olds, and three-year-olds. The user specifies the six marked points in order to define these three relationships. The default values were obtained from a synthesis of the literature (see Runge 1999).

early harvest) is modeled based on the following simple probabilistic argument. If a certain fraction, say h, of the male population is removed during the early time period, then of the reproductive females that survive that period, a fraction, $1 - h$, will still have mates and may become pregnant. This relationship is applied in the same manner across all age classes.

Parameters and equations. Two parameters directly govern litter size: the average litter size for yearlings that breed ($l_1(t)$); and the base litter size for adults ($l_A(t)$), which corresponds to the average litter size for a female age class with a relative reproductive rate of 1.0. Note that for the adult rate, the base litter size should take into account the fraction of adult females that do not successfully breed (that is, have litter sizes of 0), a fraction that is probably close to 0 in nonexploited populations. Several additional parameters are related to the fraction of young (a = 1, 2, and 3) females that breed: the number of potential sites in the area being modeled, $K(t-1)$, the maximum and minimum fraction of females of age a that breed, $b_{max}(a, t-1)$ and $b_{min}(a, t-1)$, the occupancy rate at which age a breeding begins to decline, $oc_{min}(a, t-1)$, and the occupancy rate at which age a breeding reaches its minimum, $oc_{max}(a, t-1)$. The breeding rate parameters are expressed as having occurred in the previous time period, $t-1$, since breeding occurs before the transition to the post-parturition period. A curve for relative reproductive rate as a function of age of the female, $r(a)$, needs to be defined. The final reproductive parameter is the fraction of kits born that are female, $f(t)$. Default values for the reproductive parameters are shown in Table 2.

All age classes in period 6 are advanced in period 1, thus

$$x(a,s,t,1) = x(a-1,s,t-1,6) \qquad (15)$$

for all s and $1 \leq a \leq 19$. Note that the oldest individuals in the population, $x(19,s,t - 1, 6)$, are removed from the population at this point since there is no age class 20 for them to advance to.

As noted above ("Colony structure," page 5), occupancy rate is determined at the time of the aerial survey, and is the number of active colonies divided by the number of potential sites. Thus, the occupancy rate is calculated for period 3 (of year t, say) and used in the reproduction calculations for period 1 of the next year ($t + 1$),

$$oc(t) = \frac{\sum_{a=1}^{2} b(a,t)x(a,F,t,3) + \sum_{a=3}^{19} x(a,\mathrm{F},t,3)}{K(t)} . \qquad (16)$$

The fractions of yearling, two-, and three-year-old females that potentially breed are calculated from the occupancy rate as

Table 2. Default values for reproductive parameters.

Parameter	Default Value	Source
$l_1(t)$	2.7	Henry and Bookhout (1969), Payne (1984b)
$l_A(t)$	4.5	Gunson (1967), Henry and Bookhout (1969), Payne (1984b), Dieter (1992)
$K(t)$	500	(depends on the size of the area being modeled)
$f(t)$	0.5	Hill (1982)
k	-0.006	analysis of Gunson (1967), Payne (1984b)
agemax	8.5	analysis of Gunson (1967), Payne (1984b)
$b_{max}(1, t)$	0.45	Peterson and Payne (1986)
$b_{min}(1, t)$	0.0	many, including Swenson et al. (1983)
$oc_{min}(1,t)$	0.1	intuitive estimate
$oc_{max}(1,t)$	0.4	Parsons and Brown (1979)
$b_{max}(2, t)$	0.85	Peterson and Payne (1986)
$b_{min}(2, t)$	0.0	Swenson et al. (1983)
$oc_{min}(2,t)$	0.4	intuitive estimate
$oc_{max}(2,t)$	0.9	Swenson et al. (1983)
$b_{max}(3, t)$	0.85	Peterson and Payne (1986)
$b_{min}(3, t)$	0.25	Swenson et al. (1983)
$oc_{min}(3,t)$	0.5	intuitive estimate
$oc_{max}(3,t)$	0.9	Swenson et al. (1983)

$$b(a,t) = \begin{cases} b_{\max} \\ \dfrac{b_{\min} - b_{\max}}{oc_{\max} - oc_{\min}}\left[oc(t) - oc_{\min}\right] + b_{\max} \\ b_{\min} \end{cases} \quad (17)$$

for the conditions $oc(t) < oc_{\min}$, $oc_{\min} < oc(t) < oc_{\max}$, and $oc(t) > oc_{\max}$, respectively, where it is understood that $b_{\max}$, $b_{\min}$, $oc_{\max}$, and $oc_{\min}$ are functions of a and t, with $1 \le a \le 3$ The difficulty in solving equations 16 and 17 is that they appear circular—determination of the breeding rates requires the occupancy rate, but determination of the occupancy rate requires the breeding rates for the yearling and two-year-olds. The solution is to solve these equations simultaneously for the breeding rates and calculate the occupancy rate from that. The details of this solution are not shown here, but can be found in the computer code for module 'oc_ratef.m' (Runge 1999).

The relative reproductive rate (that is, the relative litter size as a function of age of the female) is modeled with a quadratic equation,

$$r(a) = -k(a - \text{agemax})^2 + 1. \quad (18)$$

Technically, what I've been referring to as "breeding rate" above is not the breeding rate, but the fraction of females in that age class that have dispersed and established a colony by pairing with a male. Whether or not these females breed depends on the removal rate of males during the early harvest period. This removal rate is given by

$$h_M(t-1) = 1 - \frac{\sum_{a=2}^{19} x(a,M,t,4)}{\sum_{a=2}^{19} x(a,M,t,3)}. \quad (19)$$

The number of female kits born is given by

$$\begin{aligned} x(0,F,t,1) = f(t)\cdot(1 - h_M(t-1))\cdot \\ \Big[x(2,F,t,1)\cdot b(1,t-1)\cdot l_1(t) \\ + \sum_{a=3}^{4} x(a,F,t,1)\cdot b(a-1,t-1)\cdot r(a)\cdot l_A(t) \\ + \sum_{a=5}^{19} x(a,F,t,1)\cdot r(a)\cdot l_A(t)\Big] \end{aligned} \quad (20)$$

and the number of male kits born is

$$x(0,M,t,1) = x(0,F,t,1)\frac{1-f(t)}{f(t)}. \quad (21)$$

3.8 Summer nuisance control

Natural summer mortality and summer nuisance control, though simultaneous in reality, are treated as separate processes in the population model (see "Biochronology," page 3), with nuisance control occurring first (see also "Summer mortality," page 13). The transition from the *post-parturition population* ($p = 1$) to the *post-weaning population* ($p = 2$) is a result of the impact of nuisance control from the time of parturition to the beginning of the early harvest. In the northeast United States, this transition occurs between early June and late September. Unlike nuisance control during other times of the year, the removal of beavers is not unbiased across age classes. During the first two months of this time period (between parturition and weaning), the removal of a nursing mother can result in the indirect death of her kits due to starvation. Data required for this transition include: the number of non-kits removed by day during the first 60 days after parturition; the number of kits directly removed during the first 60 days after parturition; and the total number of beaver removed (kits and non-kits) from day 61 until the end of this transition. In addition, a neonate vulnerability curve is used to represent the fraction of kits that die due to the death of their mother as a function of the number of days since parturition.

Removal of non-kits pre-weaning and all beaver post-weaning. The total number of non-kits taken prior to weaning are removed proportionally across all non-kit sex/age classes. Likewise, the total number of beavers taken after weaning are removed proportionally across all sex/age classes.

Neonate vulnerability. During the 60 day period between parturition and weaning, the removal of a nursing female can result in the indirect death of her kits, with the fraction of kits that die decreasing from day 22 to day 60. The model includes a neonate vulnerability curve (Figure 5). For each nursing female removed on day d, the neonate vulnerability at day d multiplied by the average litter size determines the number of kits that are indirectly removed. The default neonate vulnerability curve postulates 50% mortality for kits orphaned at 40 days, and uses a slope parameter (0.3) that spreads the transition from 95% mortality to 5% mortality between day 30 and day 50. The details of this curve are admittedly speculative and based mainly on analogy to deer (Woodson et al. 1980), as there are no studies of this vulnerability in beaver kits.

Parameters and equations. The model requires the number of non-kits removed by nuisance control during the first 60 days after parturition by day d

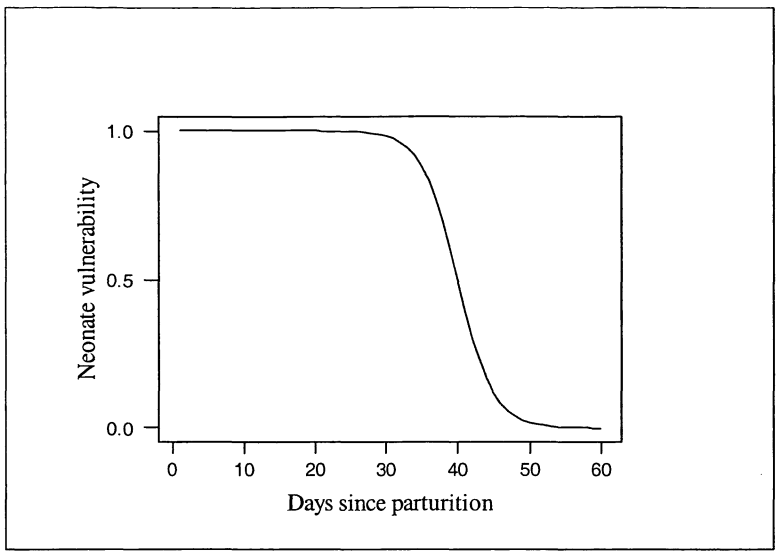

Figure 5. Neonate vulnerability curve. Neonate vulnerability is the fraction of kits that die as a result of the death of their mother. The default curve shown is a logit transform with an inflection point at d = 40 and a rate constant of 0.3 (see equation 24).

($N_{1N}(d, t)$), the number of kits directly removed during the first 60 days after parturition ($N_{1K}(t)$), and the total number of beaver removed *after* the first 60 days past parturition ($N_{1P}(t)$). The calculation is made of the fraction of the non-kit population that is females with a litter,

$$g(t) = \frac{\left(1-h_M(t-1)\right)\left[\sum_{a=2}^{4} b(a-1,t-1)x(a,F,t,1) + \sum_{a=5}^{19} x(a,F,t,1)\right]}{\sum_{a=1}^{19}\left[x(a,F,t,1)+x(a,M,t,1)\right]}. \quad (22)$$

The average litter size is given by

$$l_{avg}(t) = \frac{x(0,F,t,1)+x(0,M,t,1)}{g(t)\sum_{a=1}^{19}\left[x(a,F,t,1)+x(a,M,t,1)\right]}. \quad (23)$$

The function $nv(d)$ gives the neonate vulnerability for day d on a scale of 0 to 1, where 1 indicates that 100% of the kits die if the mother dies. The default neonate vulnerability curve is sigmoidal, designated by a logit transform function:

$$nv(d) = 1 - \frac{1}{1+e^{-0.3(d-40)}}. \quad (24)$$

The number of kits that are indirectly removed on day d as a result of the removal of their mothers is given by

$$N_{1N}(d,t)\cdot g(t)\cdot l_{avg}(t)\cdot nv(d). \quad (25)$$

Thus, the total number of female kits so removed prior to weaning is

$$\Delta x(0,F,t,2) = \sum_{d=1}^{60} f(t)\cdot N_{1N}(d,t)\cdot g(t)\cdot l_{avg}(t)\cdot nv(d) \quad (26)$$

and the total number of male kits removed is

$$\Delta x(0,M,t,2) = \sum_{d=1}^{60}\left(1-f(t)\right)\cdot N_{1N}(d,t)\cdot g(t)\cdot l_{avg}(t)\cdot nv(d). \quad (27)$$

Some kits are also removed directly during this suckling period, and are merely subtracted from the kit population.

During the 60-day lactation period, the total number of non-kits removed is subtracted proportionally from the non-kit population. The removal *rate* for the pre-weaning interval is

$$n_{1pre}(t) = \frac{\sum_{d=1}^{60} N_{1N}(d,t)}{\sum_{a=1}^{19} x(a,F,t,1)+x(a,M,t,1)}. \quad (28)$$

During the remainder of the transition from period 1 to period 2, the total number of beavers removed is

subtracted proportionally from the population. The removal rate for the post-weaning interval is

$$n_{1post}(t) = \frac{N_{1P}(t)}{\left[\begin{array}{l}\sum_{s=F}^{M}\sum_{a=0}^{19} x(a,s,t,1) \\ -\sum_{d=1}^{60} N_{1N}(d,t) \\ -N_{1K}(t) - \Delta x(0,s,t,2)\end{array}\right]}. \quad (29)$$

The number of female kits alive at period 2 is

$$x(0,F,t,2) = \left(1 - n_{1post}(t)\right)\cdot \left[x(0,F,t,1) - \Delta x(0,F,t,2) - f(t)\cdot N_{1K}(t)\right], \quad (30)$$

the number of male kits alive at period 2 is

$$x(0,M,t,2) = \left(1 - n_{1post}(t)\right)\cdot \left[x(0,M,t,1) - \Delta x(0,M,t,2) - \left(1 - f(t)\right)\cdot N_{1K}(t)\right], \quad (31)$$

and for all s and $1 \le a \le 19$, the number of beaver alive at period 2 is

$$x(a,s,t,2) = \left(1 - n_{1post}(t)\right)\cdot\left(1 - n_{1pre}(t)\right)\cdot x(a,s,t,1) \quad (32)$$

3.9 Summer mortality

The transition from the *post-weaning* (p = 2) to the *pre-harvest population* (p = 3) is a result of the impacts of summer mortality, which includes mortality due to dispersal. In the northeast United States, this transition occurs from early June to early October. The model requires minimum (low-density) mortality rates for male and female kits, yearlings, two-year-olds, three-year-olds, and adults; maximum (high-density) mortality rates for two- and three-year-olds; and a function that relates dispersal mortality to pre-dispersal occupation rate for two- and three-year-olds. The vulnerability curve used for relative adult mortality rates is the same as that used in the winter mortality calculations (see "Winter mortality," page 7).

Density-dependence of dispersal mortality. Beaver typically disperse from their natal colony in their third or fourth summer (as two- or three-year olds). If the colony density is low and they are able to find a suitable site (and mate) to establish a colony, they become part of the breeding population. If the colony density is high they are more likely to die from starvation, predation, or accident as they search for a site. To compensate for this, when the colony density is high, beaver (especially two-year-olds) may delay dispersal for another year. We might expect the summer mortality of dispersers to look like Figure 6. At very high occupancy rates, about half of the two-year-olds disperse (Brooks et al. 1980), are unable to find sites, and eventually die (thus, a maximum mortality of around 0.5). At these same high densities, any three-year-olds alive will still be in the natal colony, will all disperse, and most (0.85) will die (see Molini et al. 1981). The range over which the density-dependence of dispersal mortality acts (a to b in Figure 6) is not estimated in the literature. The default values used herein are based on the intuitive arguments that the occupancy rate has to be fairly high (certainly above 0.5) before this density-dependence is evident, and that the change from minimum to maximum mortality should not be abrupt.

Parameters and equations. Default values are shown in Table 3 for the mortality rates for male and female kits, $ms(0, M, t)$ and $ms(0, F, t)$, yearlings, $ms(1, M, t)$ and $ms(1, F, t)$, and adults, $ms_{AM}(t)$ and $ms_{AF}(t)$. The minimum and maximum summer mortality rates for two-year-olds are given by $ms_{min}(2, s, t)$ and $ms_{max}(2, s, t)$, and are defined analogously for three-year-olds. Vulnerability curves for male and female adults are specified by equation 10.

Table 3. Default summer mortality rates. For two- and three-year-olds, the minimum and maximum mortality rates are shown. The default values for kits are based on Gunson (1970) and those for yearlings are based on Svendsen (1980). The minimum two-year-old mortality is loosely based on Boyce (1981) and Gunson (1970) and reflects the observations that males face slightly greater risks during this period (Leege 1968, Novak 1987a). The adult and minimum three-year-old mortality rates are set at a value that is about in the middle of the wide range of estimates for these rates (Payne 1984a, Boyce 1981, Hodgdon 1978, Molini et al. 1981). See text for justification of the maximum mortality rates for two- and three-year-olds. The default values for a_{disp} and b_{disp} are 0.65 and 0.9, respectively.

Sex\Age	0	1	2	3	Adult
Male	0.027	0.016	0.095 – 0.50	0.03 – 0.85	0.03
Female	0.027	0.016	0.075 – 0.50	0.03 – 0.85	0.03

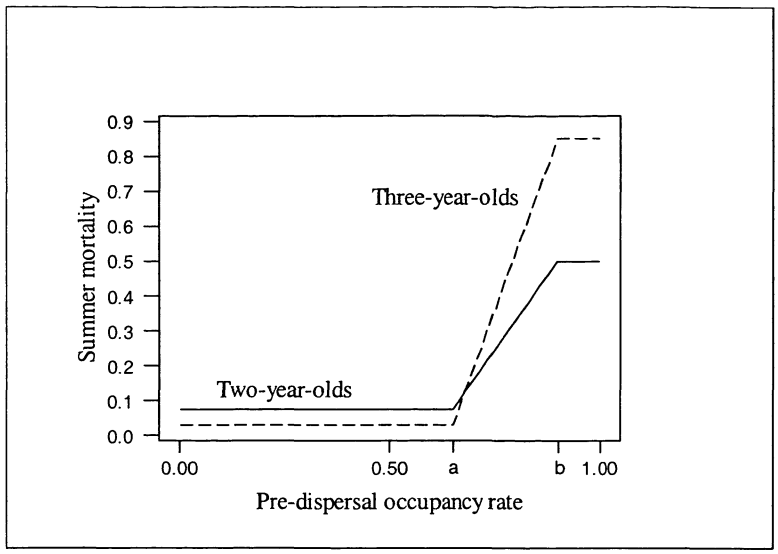

Figure 6. Summer mortality for two- and three-year-olds as a function of occupancy rate. At higher population densities, there are fewer available colony sites and dispersing beaver may succumb to various sources of mortality before finding a site.

The pre-dispersal occupancy rate (as opposed to the occupancy rate at the time of the aerial survey, which is *post*-dispersal) depends on the potential breeding rates for the previous reproductive season, which in turn, depend on the post-dispersal occupancy rate in the previous fall. Thus,

$$oc_{\mathrm{Pre}}(t) = \frac{\sum_{a=2}^{3} b(a-1,t-1)x(a,F,t,2) + \sum_{a=4}^{19} x(a,F,t,2)}{K(t)} \tag{33}$$

describes the pre-dispersal occupancy rate. The summer mortality rates for two- and three-year-olds are given by

$$ms(a,s,t) = \begin{cases} ms_{\min}(a,s,t) \\ \dfrac{ms_{\max}(a,s,t) - ms_{\min}(a,s,t)}{b_{\mathrm{disp}} - a_{\mathrm{disp}}}\left[oc_{\mathrm{Pre}}(t) - a_{\mathrm{disp}}\right] \\ \qquad + ms_{\min}(a,s,t) \\ ms_{\max}(a,s,t) \end{cases} \tag{34}$$

depending on whether $oc_{\mathrm{Pre}}(t) < a_{\mathrm{disp}}$, $a_{\mathrm{disp}} \le oc_{\mathrm{Pre}}(t) \le b_{\mathrm{disp}}$, or $oc_{\mathrm{Pre}}(t) > b_{\mathrm{disp}}$, respectively. The period 3 population is calculated with

$$x(a,s,t,3) = x(a,s,t,2)\cdot\left(1 - ms(a,s,t)\right), \tag{35}$$

for all s and for $a \le 3$, and with

$$x(a,s,t,3) = x(a,s,t,2)\cdot\left(1 - ms_{As}(t)\cdot v_s(a)\right) \tag{36}$$

for all s and for $a > 3$, subject to the constraint that

$$ms_{As}(t)\cdot v_s(a) \le 1\,. \tag{37}$$

3.10 Environmental stochasticity

The model described thus far is strictly deterministic, with all parameters that are a function of t being interpreted as constants which might change from year to year, but only as specified by the user. A deterministic approach is useful for making point predictions of the population size and for exploring dynamics that arise out of the deterministic structure of the model, such as the sensitivity of the growth rate to changes in the parameters. A stochastic approach is required, however, when prediction intervals are needed, when the level of uncertainty about population growth needs to be assessed, and when it is desirable to simulate population growth under fluctuating environmental conditions. To incorporate environmental stochasticity, some of the parameters would have to be represented as random variables. To simulate environmental stochasticity in winter mortality, for instance, the ten winter mortality rates, ($mw(a, s, t)$ for $a \le 3$ and $mw_{\mathrm{As}}(t)$), could be treated as a random vector, with a specified mean, variance-

covariance structure, and joint probability distribution. A similar procedure could be used with the summer mortality. To simulate environmental stochasticity in reproduction, the litter sizes for adults and yearlings that breed could be treated as random variables with specified probability distributions.

3.11 Aspects not *included*

Models representing natural populations cannot be complete and totally realistic. Often population models cannot even approach such a goal without being unwieldy and intractable. Tradeoffs between realism, precision, and generality are unavoidable in any modeling context (Levins 1966). It is important that a modeler be aware of what has been left out. The four most important aspects left out of the beaver population model described above are demographic stochasticity, late-winter starvation, colony structure, and other relationships between the variables.

When populations are large, the effects of demographic stochasticity are small. Since the beaver population model is designed to be used at the management unit level, where the population is high enough that a harvest is justified, the absence of demographic stochasticity is probably warranted. However, because there are so many sex/age classes, even with a large population some of the sex/age classes may have very few individuals in them, and so the effects of demographic stochasticity may be important in those classes. On the other hand, since the sex/age classes which will have the smallest numbers will be the older adults, for whom mortality is relatively high and reproductive rates are low, this effect may be negligible.

An additional source of mortality for beavers is late-winter starvation. This can occur when the under-ice period is long and the food cache becomes exhausted before the ice breaks. Modeling this mortality can be approached from a bioenergetics viewpoint (Moen 1973), focusing on the typical cache and how long it could be expected to last for a colony of a particular composition. There is a mechanism for compensatory harvest mortality here—trapping will reduce the number in the colony, freeing up food resources for the remaining members. Thus, mortality due to trapping may be at least partially compensated by reduction in the potential for late-winter starvation. The timing of the trapping certainly plays a role, as the earlier a beaver is removed, the more food resources are left for the rest of the colony. The timing of removal is most important at more northern latitudes, where the under-ice period is long and continuous. In the middle and southern portions of their range, beaver are not typically confined under-ice for the entire winter, and have an opportunity to forage during intermittent breakups. This may be an important addition to the model for populations in colder climates.

Since females can pheromonally repress reproduction in younger females in the same family unit, careful consideration should be given to colony structure in a beaver population model. I have included the effect of colony structure on reproduction, through the indirect method of having reproductive rates depend on occupancy rate, but a full-fledged treatment of this dynamic would need to track individuals with regard to their "colony status." The problem is that modeling colony *structure* (not just number of colonies) along with sex/age structure increases model complexity considerably—for a given sex/age distribution, there may be many different colony structures possible. For such a model to be meaningful, the manager would have to collect data on aspects of colony structure—for instance, each beaver harvested would have to be associated with a particular colony and would also need to be sexed and aged. Since such detailed data are both expensive and hard to come by (and thus are unlikely to be gathered), a model that included such colony structure would appear to be very realistic, but that level of detail would not be justified, as there would be no feedback to adjust the model's predictions in regard to colony structure.

Finally, this model does not include a number of other relationships among the variables. For instance, the sex ratio of the kits is not tied to any other variable, like the occupancy rate or the age of the mother. In some species, for example, white-tailed deer (Moen et al. 1986), such relationships are important. Another factor that has been discussed in regard to beaver population dynamics is the epidemiology of wide-spread disease, especially tularemia (Stenlund 1953, Lawrence et al. 1956), which may be density-dependent. It is my belief that I have not, however, left out any relationship that is critical to a population model of beaver.

4 Dynamics of this Population Model

In this section, I explore population dynamics with the beaver model, looking for properties that arise at the population level from the synthesis of more basic processes. For dynamics for which field observations are available, agreement or discrepancy between model dynamics and known dynamics can support or undermine confidence in the model structure. For dynamics for which field observations are *not* available, the model can be used to generate field-testable hypotheses.

4.1 Methods

Two major methods were used to investigate the dynamics of this model, one that looked at the long-term equilibrium properties, and one that looked at "instantaneous equilibrium" properties. In the first method (long-term equilibrium), an initialized population was allowed to increase or decrease over time, under a certain set of conditions, until the population size and structure reached stable levels. Both the trajectory over time and the final equilibrium state were of interest. In the second method (instantaneous equilibrium), an initialized population was allowed to grow for one year under a certain set of conditions, then the final sex/age distribution was applied to the initial population size, and the process was repeated 50 to 150 times until a stable structure was obtained for that particular starting population size. Unless noted otherwise, default values were used for all parameters, the carrying capacity of the environment was 500 colonies, and there was no removal of animals by nuisance control. Four specific experiments were conducted.

In the first experiment ("growth of a nonexploited population over time"), the long-term equilibrium method was applied to an initial population of size 10. This initial population had a stable sex and age structure, produced by applying the more detailed initialization procedure (which is equivalent to the instantaneous equilibrium method). Note that fractions of an animal were possible in any particular sex/age class. The population model was used to simulate the growth of the initial population over a period of 50 years, in the absence of harvest or nuisance control. The total population size and structure were recorded for each point in time.

In the second experiment ("growth rates, occupancy rates, and average colony size"), the instantaneous equilibrium method was applied to initial population sizes from 100 to 4500 in increments of 200, in the absence of harvest or nuisance control. From the stable population structure produced by this method, the growth rate and the fall and summer occupancy rates were calculated. The growth rate was the fractional increase in the population size after one year, that is,

$$\frac{n_{t+1}}{n_t} - 1 \tag{38}$$

where n_t is the total population size at time t. The fall and summer occupancy rates were calculated using equations 16 and 33. The average colony size was calculated by dividing the pre-harvest population size by the product of the fall occupancy rate and the colony carrying capacity,

$$\text{Average colony size} = \frac{\sum_s \sum_a x(a,s,t,3)}{oc(t) \cdot K(t)}. \tag{39}$$

In the third experiment ("effect of harvest on growth rate"), the instantaneous equilibrium method was applied in the same way as in the second experiment, only this time harvest was included. Early or late harvest rates of 0 to 0.4, in increments of 0.1, were applied to populations of size 100 to 4500, in increments of 200. Growth and occupancy rates were calculated as above. In addition, an *adjusted* growth rate was also calculated to measure the growth of the population after accounting for the effect of harvest. This adjusted growth rate was calculated as

$$\frac{n_{t+1}}{n_t(1-h)} - 1, \tag{40}$$

where h is the harvest rate in relation to the pre-harvest ($p = 3$) population size.

In the fourth experiment ("effect of harvest on stable population size and structure"), the long-term equilibrium method was applied to an initialized population that was experiencing a constant harvest rate. Large initial population sizes were chosen so that the population started out at full occupancy, and the model was run until the population reached a stable size and structure. The early and late harvest rates used were 0, 0.05, 0.10, 0.15, and 0.20 to 0.34 in steps of 0.01 (note that a harvest level of 0 corresponds to the first experiment). The final stable size, occupancy rate, and average colony size were recorded.

4.2 Results and discussion

The results of these four experiments, discussed in detail below, suggest that the model structure is realistic, since the dynamics of the model qualitatively match observed dynamics. There is, however, a suggestion that the default parameter estimates produce a growth rate that is too high. Several interesting dynamics involving average colony size and the effect of harvest have not been studied in the field, and provide testable hypotheses for future studies.

Growth of a nonexploited population over time. The model exhibits density-dependent growth of the total population size, with fast growth at low population size being reduced to zero growth at high population size (Figure 7). It takes about 25 years for the simulated population to reach a stable population

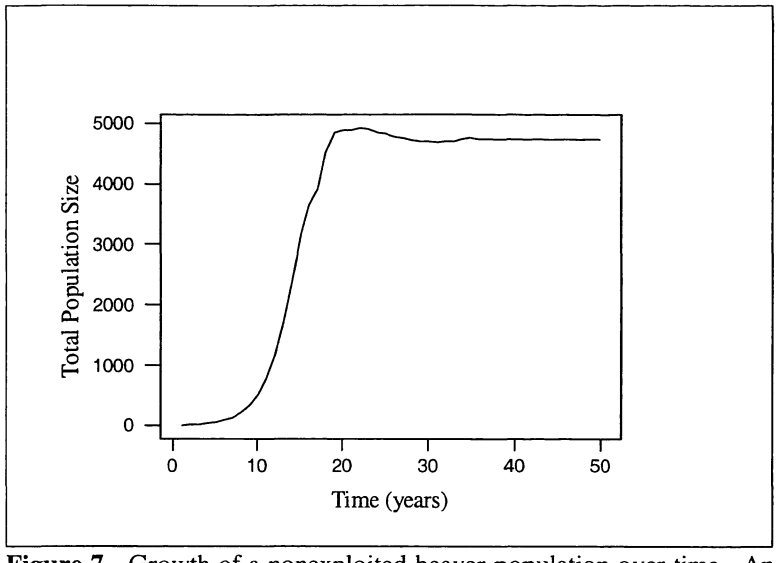

Figure 7. Growth of a nonexploited beaver population over time. An initial population size of ten, with a stable age-structure, was used. The number of potential colony sites in the area being modeled was set at 500.

size, that is, to "saturate" the potential habitat. Lancia and Bishir (1985) show data from a nonexploited population in Massachusetts that grew from 3 individuals in 1952 to around 300 in 1975, at which point it seemed to have reached a stable level. That is, the observed population took 23 years to increase by two orders of magnitude. The simulated population took about 12 years to increase by two orders of magnitude (from 10 to 1000). Thus, the population growth was qualitatively like that seen in the field, but the intrinsic growth rate in the model may be too high, at least in comparison to the beaver population in this area of Massachusetts.

Notable changes in the age structure of the simulated population occurred over time (Figure 8). The kit and three-year-old fractions declined, while all other age classes increased in relative abundance. The decrease in the kit fraction is due to the density-dependent reduction in reproductive rates of younger females. The decrease in the three-year-old fraction is due to density-dependent dispersal mortality. The fractions seen in the simulated population match those reported in the literature fairly well. The kit and yearling fractions at saturation are on the high end of observed values (Hill 1982, Novak 1987a), suggesting that the reproductive rates are higher in the model than are typical in nature. Density-dependent effects produced some sharp jumps in the age-structure trajectories, a property that is typical of natural populations in which reproduction occurs only

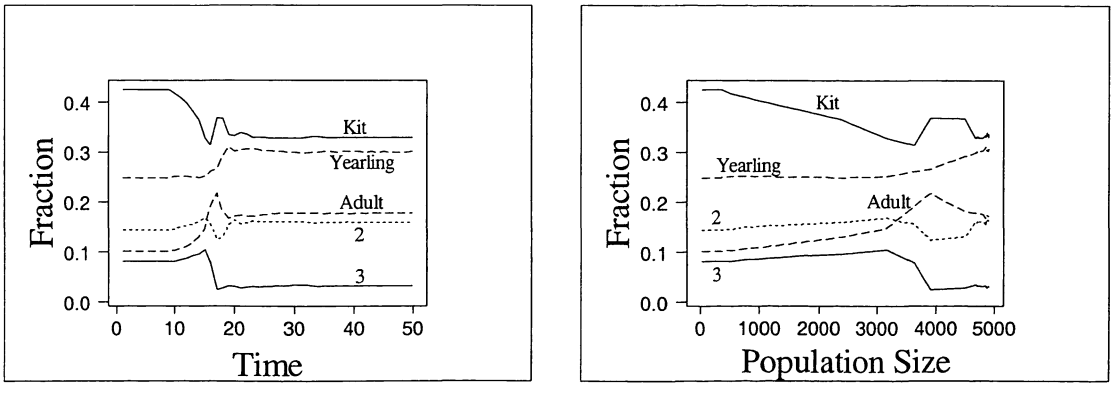

Figure 8. Age-structure of a simulated beaver population over time. The fraction of the population in several age classes is shown relative to time and total population size.

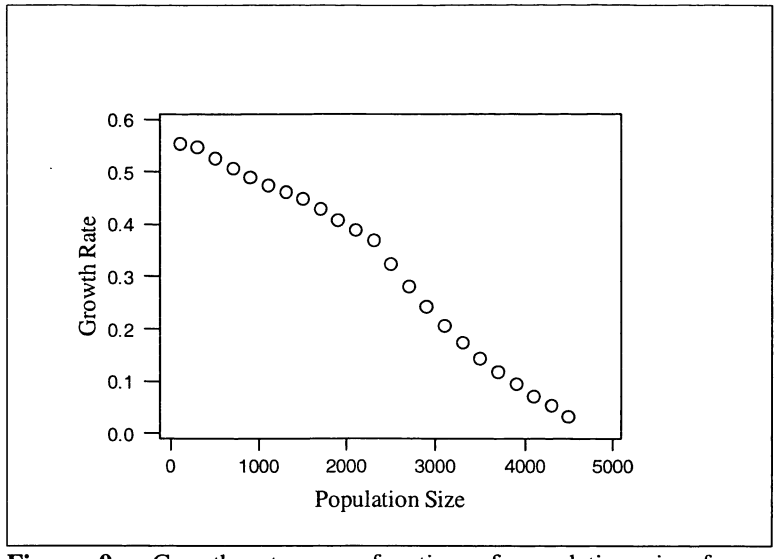

Figure 9. Growth rate as a function of population size for an unharvested population.

once per year.

Growth rates, occupancy rates, and average colony size. The instantaneous growth rate as a function of population size is shown in Figure 9. The relationship between growth rate and population size is not linear across the full range of population sizes (as would be expected under a simple logistic model). Rather, there appears to be an abrupt change in slope near a population size of 2300. This corresponds to pre-dispersal and post-dispersal occupancy rates of 0.65 and 0.72, respectively, which is where the density-dependent effect of dispersal mortality begins. When the growth rate is plotted against the *occupancy rate* it can be seen more clearly that the sharp change in slope corresponds to the lower threshold of density-dependence in dispersal mortality (Figure 10a). The intrinsic rate of increase, as measured by the y-intercept of the curve in Figure 9, is near 0.55, higher than that estimated by Lancia and Bishir (1985), who argued that a range of 0.35 to 0.45 was reasonable. This discrepancy, and the high kit fraction in Figure 8, could indicate that the base adult litter size (l_A) is too large. I would not expect the qualitative dynamics of this model to be changed, however, by adjustment of this parameter.

Occupancy rate increases with increasing population size, though not in a linear fashion—the slope of the relationship is greater for lower population sizes than it is for higher ones (Figure 10b). Thus, a post-dispersal occupancy rate of 0.5 corresponds to a population size of about 1500, while an occupancy rate of 1 corresponds to a population

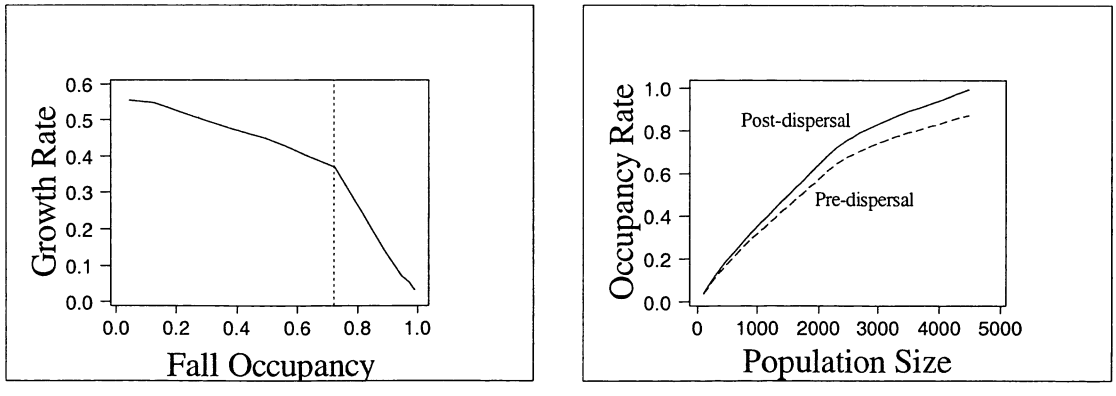

Figure 10. Growth rate, occupancy rate, and population size. (a) In the first graph, the growth rate is plotted against the fall occupancy rate. The change in slope occurs at a fall occupancy rate of 0.72, which corresponds to a summer occupancy rate of 0.65. (b) In the second graph, the pre-dispersal (summer) and post-dispersal (fall) occupancy rates are plotted against population size.

size of near 5000. Note that the pre-dispersal (summer) occupancy rate is always lower than the post-dispersal (fall) occupancy rate, and never reaches 1. This makes sense—prior to dispersal, there are a number of available colony sites, vacated as a result of mortality over the previous year. At saturation, the occupancy rate *post-dispersal*, however, should be 1, as the open sites are filled by dispersing beaver.

If the occupancy rate and the population size do not change in a linear fashion, then the average colony size must not be constant across all conditions (Figure 11). In fact, the average colony size increases steadily with increasing occupancy, reflecting the observation that beaver delay dispersal at higher population densities. The graph of colony size against occupancy shows distinct linear segments, which correspond to the occupancy ranges in which different dynamics are acting. (In the discussion to follow, occupancy rate refers to the fall occupancy rate unless otherwise noted, and is designated as *oc*.) Below $oc = 0.1$, the maximum fraction of yearlings, two-, and three-year-olds breed. Between $oc = 0.1$ and 0.4, the breeding of yearlings is reduced to zero. The colony size increases for two reasons: yearlings are staying in the natal colonies rather than dispersing, and the average litter size is higher for non-yearling breeders. At $oc = 0.4$, the breeding of two-year-olds begins to decline, and at $oc = 0.5$, the breeding of three-year-olds begins to decline. Both breeding rates are reduced to a minimum at $oc = 0.9$. The two-year-old effect is to increase colony size for the same reason as for yearlings. In and of itself, the three-year-old effect should be to *decrease* colony size, since three-year-olds are considered to have all dispersed by the breeding season, and thus, reduction of their breeding rate means there are an increased number of pair and single colonies. Note that this effect is seen as a smaller slope in the range $oc = 0.5$ to 0.72, than in the range 0.4 to 0.5. Finally, at $oc = 0.72$ (corresponding to summer occupancy of 0.65), the average colony size begins to increase markedly, because the two-year-olds are delaying dispersal, and the two- and three-year-olds that do disperse are facing heavy mortality. Thus, most colonies consist of breeding adults with their kits, yearlings, and undispersed two-year-olds.

These occupancy rate dynamics in the population model suggest a discrepancy, a field experiment, and a caution to managers. First, the graph of average colony size (Figure 11) reveals a problem with the model structure—the transitions between different density-dependent dynamics are more abrupt than should be expected in a natural population. I've represented density-dependent effects on breeding and dispersal as simple linear relationships, when they are probably much more complicated. Second, this same graph suggests a field-testable hypothesis—colony sizes will increase with increasing occupancy. While the range of average colony sizes produced by the model closely matches that reported in the literature (Novak 1987a), I know of no study that has specifically looked at the relationship between colony size and occupancy rate. Such a study could be done

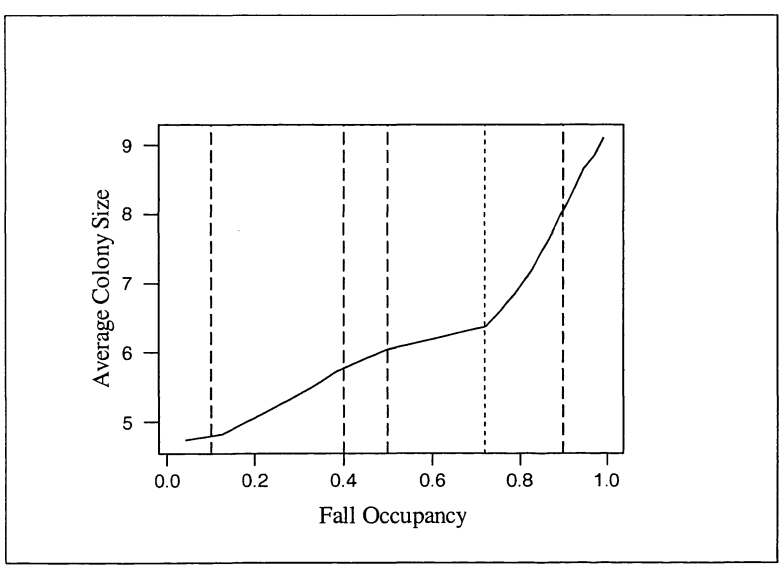

Figure 11. Average colony size as a function of fall occupancy rate. The dashed reference lines are at fall occupancy rates of 0.1, 0.4, 0.5, and 0.9. The dotted reference line is at a fall occupancy rate of 0.72, which corresponds to a summer occupancy rate of 0.65.

through manipulation of occupancy rates in a number of districts, or through meta-analysis of state, provincial, and private data. Third, an important caution to managers—it is dangerous to assume that colony size is constant. In fact, there is strong reason to believe that average colony size can change considerably, undermining how a manager combines aerial survey estimates of colony density with harvest rates when making population projections.

Effects of harvest. The effect of harvest on population dynamics, especially the short- and long-term growth rates, are of crucial importance to the endeavor to manage beaver. The results of the third and fourth experiments follow.

On growth rate. The gross growth rate expected for a population depends both on the population density and on the harvest rate (Figure 12). Several aspects of this relationship are of interest. First, increasing the early harvest rate by 0.1 decreases the growth rate by *more than* 0.1, because early harvest of males reduces the pregnancy rate (see below for discussion of early versus late harvest). Second, harvest rates of 10-20% are not enough to stop the growth of a beaver population (unless the population is at full occupancy, in which case its growth is stopped naturally). Third, the range of harvest rates relevant for management is fairly narrow, say, between 25% and 35%—this is where growth rates are zero over the range of desirable occupancy levels.

To make a more direct comparison of different harvest levels, consider the *adjusted* growth rate as a function of population size (Figure 13). The adjusted growth rate relationship for a harvested population is similar to that of an unharvested population, with several notable differences. At low density, the adjusted growth rates under early and late harvest scenarios are lower than with no harvest, but for different reasons. In the case of early harvest, removal of males reduces the pregnancy rate of the remaining females, hence, there is less reproduction. In the case of late harvest, the winter mortality is a greater fraction of the *adjusted* population size, n_t (1 – h), since it occurs prior to the harvest. The relative impact of these two dynamics changes over the full range of population density. At high densities, the adjusted growth rate under a harvest scenario is *higher* than with no harvest, because of a compensatory interaction between harvest mortality and dispersal mortality. At high density, harvest opens up colony sites, reduces the pre-dispersal density, and allows dispersers to find sites.

On stable population size and structure. The stable population size produced by harvesting at a constant rate over time decreases steadily with increasing harvest rate, and is zero for an early harvest rate of 0.32 or a late harvest rate of 0.34 (Figure 14). Note this is a fixed *rate*, not a fixed total harvest. Thus, an early harvest rate of 32% or above is not sustainable. The average colony size in an equilibrium population also decreases steadily with increasing harvest rate.

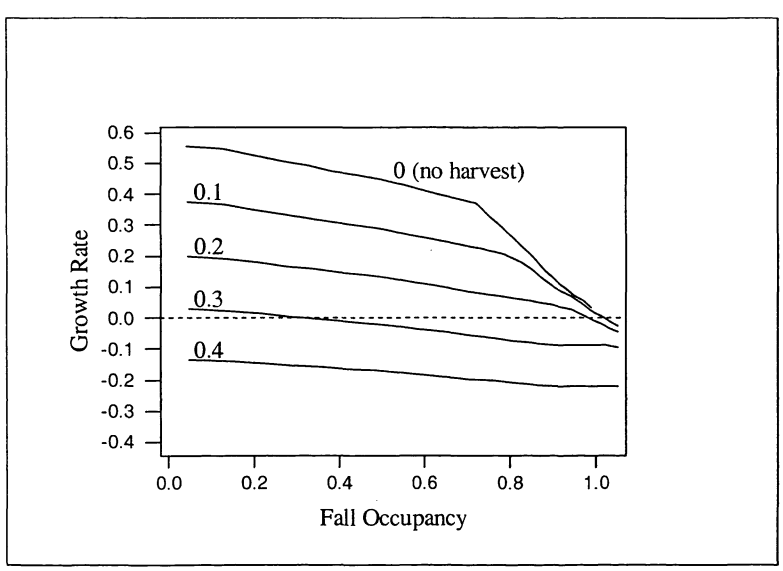

Figure 12. Finite growth rate as a function of fall occupancy, for a range of harvest rates. The harvest rates shown are expressed as a fraction of the pre-harvest population (p = 3). This graph shows the results for the case where there is *early* harvest only. The results for late harvest are qualitatively similar.

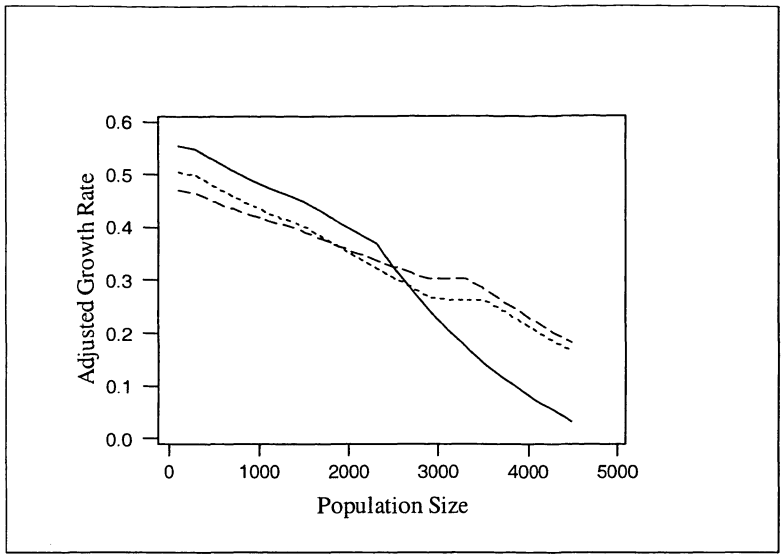

Figure 13. Adjusted growth rate (equation 40) as a function of population size. The solid line is for a harvest rate of 0, the dashed line is for an *early* harvest rate of 0.3, and the dotted line is for a *late* harvest rate of 0.3, where the harvest rate is always measured relative to the pre-harvest population size.

The most interesting result is the effect of harvest rate on the stable occupancy rate (Figure 15). For sustained harvest rates below 20%, there is *no reduction* in the occupancy rate. The removal of beavers creates space for dispersers. Since the dispersers initially have smaller colonies, the average colony size and the total population size are smaller, but the potential sites remained filled. As the harvest rate rises above 21-23%, the summer occupancy rate drops below the dispersal mortality threshold (0.65) and the compensatory effect is removed. Increases in harvest above this rate result in a sharp decrease in the stable occupancy rate. This decrease begins at a lower rate for late harvest, because of the interaction with winter mortality noted above, but is steeper for early harvest, because of the effect on pregnancy rate. In either case, the range of sustained harvest rates desirable for management is quite narrow. This means that in the range of occupancy rates typically sought through management, the population size and occupancy rate are quite sensitive to harvest. Thus, harvest management can be an effective tool.

5 Parameter Estimation and Sensitivity Analysis

In this section I analyze the sensitivity of the population growth rate to changes in the model parameters over ranges that capture what has been reported in the literature. Such a sensitivity analysis is one of the most useful applications for a detailed population model because it helps prioritize research objectives by identifying those parameters that are most important to estimate precisely. In the

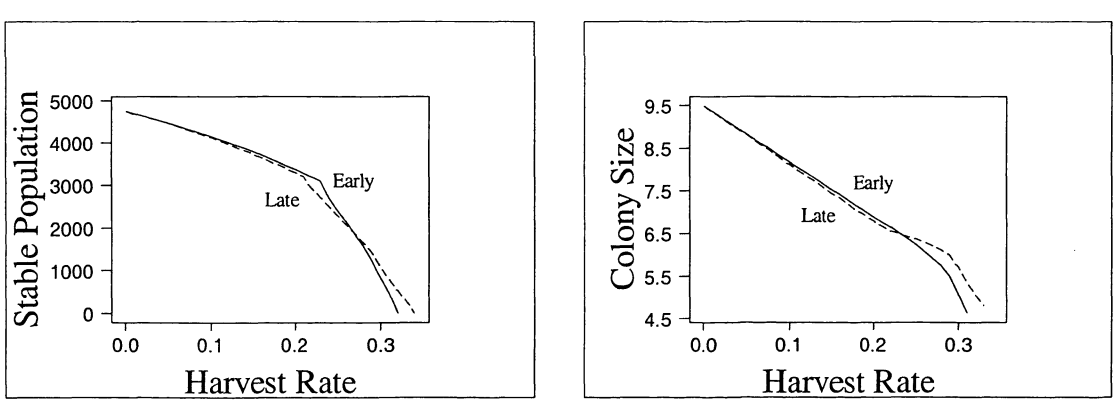

Figure 14. Stable population size and colony size as a function of harvest rate. Results using early harvest only are shown with a solid line, late harvest only with a dashed line.

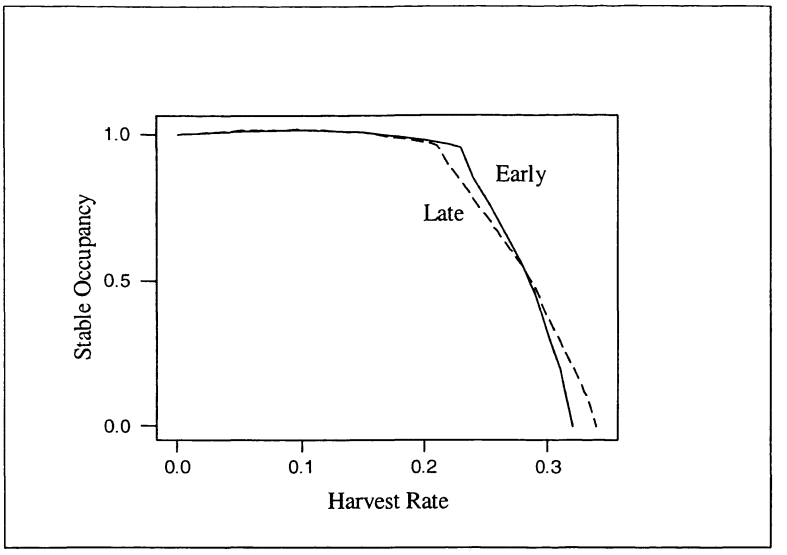

Figure 15. Stable fall occupancy rate as a function of harvest rate. The decline with early harvest spans rates of 0.23 to 0.32. The decline with late harvest spans rates of 0.21 to 0.34.

preceding model development and analysis, I have used the literature on beaver life history to suggest reasonable values for the parameters, but many of the parameters have never been measured directly or cannot even be measured properly. Most of the parameters that *have* been measured show large variations between studies. The sensitivity analysis will show, however, that most of the model parameters do not need to be specified with great precision, as they have only minor effects on the population dynamics. A manager's top priority in regard to understanding a beaver population should be in estimating those parameters that are identified as having a very strong effect on population dynamics.

The approach taken was to choose combinations of the parameters from independent uniform distributions and calculate the stable growth rate associated with each combination (Wisdom and Mills 1997). Because there are strong density-dependent effects, this process was repeated at three different densities. Then, the importance of the parameters in affecting the growth rate was ranked using several regression techniques (Wisdom and Mills 1997). This method differs from an elasticity analysis in that the ranking depends both on the elasticity of the parameter *and* on the range of possible values (or variance) for that parameter. Thus, for instance, a parameter with a high elasticity but no uncertainty in its estimate would not appear as significant.

5.1 Methods

Forty-seven of the parameters described above were chosen for investigation (Table 4) and the remaining ones were fixed at the default values. Two were fixed because the model is overspecified (c_1(F) and c_1(M)), two were fixed because the evidence clearly supports the default values ($b_{min}(1)$ and $b_{min}(2)$), and the remaining ones were not relevant to the sensitivity analysis (the kit and harvest vulnerability parameters), since the harvest and nuisance control rates were set at zero. For the parameters investigated, a plausible range was specified based on values reported in the literature (Table 4). Random combinations of these 47 parameters were chosen by drawing each independently from a continuous uniform distribution with the range specified.

For each replicate, a random combination of parameters was generated, and the stable growth rate was calculated by a method analogous to the power method used in matrix model analysis (Caswell 1989). To do this, the population model was repeatedly run for one time step (year) with the specified parameter combination, each time readjusting the starting sex/age structure, until the stable structure was found for that parameter combination. The growth rate was then expressed as an exponential growth rate, i.e., as $\ln(N_{t+1}/N_t)$. This entire process was repeated 2500 times at each of three population densities (100, 800, and 3500 individuals in a region with $K = 500$ colony sites).

At each density, two methods were used to identify and rank parameters that had a significant

Table 4. Sensitivity analysis parameters. For the sensitivity analysis, each parameter was chosen independently from a uniform distribution with the range shown. The exponential growth rate, $\ln(N_{t+1}/N_t)$, was calculated for each of 2500 replicates. The last 3 columns show the coefficients of determination for the simple linear regressions of growth rate on each parameter. Only the ten (six for N_t = 3500) parameters with the highest R^2 values are shown. The sign (+ or –) indicates whether there was a positive or negative correlation between growth rate and that particular parameter. Any parameter for which a sign is not shown was not significantly correlated with growth rate. At the bottom of the table, the R^2 values are shown for the multiple regressions of growth on all 47 parameters. († The c_2 vulnerability values are shown on the ln-scale.)

Parameter	**Range**	**Individual R^2**		
		N_t = **100**	N_t = **800**	N_t = **3500**
Winter Mortality				
mw(0, F)	(0.015, 0.25)	13.4 % (–)	7.5 % (–)	(–)
mw(0, M)	"			1.4 % (–)
mw(1, F)	(0, 0.1)	2.3 % (–)	1.5 % (–)	
mw(1, M)	"			(–)
mw(2, F)	(0, 0.2)	4.6 % (–)	4.8 % (–)	
mw(2, M)	"			(–)
mw(3, F)	"	(–)	2.0 % (–)	
mw(3, M)	"			
mw_{AF}	"	4.6 % (–)	5.9 % (–)	(–)
mw_{AM}	"		(+)	(–)
Summer Mortality				
ms(0, F)	(0, 0.054)	(–)	(–)	(–)
ms(0, M)	"			
ms(1, F)	(0, 0.032)	(–)	(–)	
ms(1, M)	"			
ms_{min}(2, F)	(0.01, 0.14)	2.1 % (–)	(–)	
ms_{min}(2, M)	(0.03, 0.16)			
ms_{min}(3, F)	(0, 0.05)		(–)	
ms_{min}(3, M)	"			
ms_{AF}	"	(–)	(–)	
ms_{AM}	"			(–)
Vulnerability				
c_1(F)	**fixed**			
k_1(F)	(–0.08, 0.18)		(–)	
c_2(F)	(–20.9, –13.5) †			
k_2(F)	(0.5, 1.5)			
c_1(M)	**fixed**			
k_1(M)	(–0.08, 0.18)		(+)	
c_2(M)	(–20.9, –13.5) †			
k_2(M)	(0.5, 1.5)			
Reproduction				
l_A	(3.0, 6.0)	43.5 % (+)	51.9 % (+)	60.2 % (+)
l_1	(2.1, 3.3)	(+)		
f	(0.46, 0.54)	3.9 % (+)	2.1 % (+)	
k	(–0.010, –0.002)	4.5 % (+)	4.7 % (+)	1.6 % (+)
agemax	(6, 11)	6.6 % (–)	8.0 % (–)	(–)

impact on growth rate. First, those parameters that were significantly correlated with growth rate were ranked by the magnitude of that correlation (this is equivalent to ranking by the R^2 values of the regressions of growth rate on each parameter individually). Second, stepwise regression of growth rate on all the parameters was performed, and ranks were assigned based on the order in which parameters were added to the regression model (the F-value to add a variable to or remove one from the model was

Table 4 (Continued). Sensitivity analysis parameters.

Parameter	Range	Individual R^2		
		$N = 100$	$N = 800$	$N = 3500$
Breeding Rates				
$b_{max}(1)$	(0.25, 0.65)	5.0 % (+)	(+)	
$b_{min}(1)$	**fixed**			
$oc_{min}(1)$	(0, 0.2)		(+)	
$oc_{max}(1)$	(0.2, 0.6)		3.1 % (+)	
$b_{max}(2)$	(0.7, 1.0)	(+)	(+)	
$b_{min}(2)$	**fixed**			
$oc_{min}(2)$	(0.2, 0.6)			
$oc_{max}(2)$	(0.8, 1.0)			
$b_{max}(3)$	(0.7, 1.0)	(+)	(+)	
$b_{min}(3)$	(0.1, 0.4)			(+)
$oc_{min}(3)$	(0.3, 0.7)			
$oc_{max}(3)$	(0.8, 1.0)			
Kit Vulnerability				
(slope)	**fixed**			
(midpoint)	**fixed**			
Dispersal Mortality				
$ms_{max}(2, F)$	(0.3, 0.7)			
$ms_{max}(2, M)$	"			1.4 % (–)
$ms_{max}(3, F)$	(0.75, 0.95)			
$ms_{max}(3, M)$	"			(–)
a_{disp}	(0.5, 0.8)			2.1 % (+)
b_{disp}	(0.8, 1.0)			3.7 % (+)
Total	47 + 6 fixed	97.3 %	97.2 %	75.1 %

4.0). A composite ranking was obtained by sorting the parameters according to the sum of the two rankings described above, retaining only those parameters that were significant with regard to both criteria.

5.2 Results

At all population densities, the adult litter size (l_A) was the most important determinant of growth rate, no matter what ranking method was used (Tables 4 and 5). Variation in this parameter explained between 43% and 60% of the variation in the growth rate. No other single parameter came anywhere near explaining this level of variation. Other parameters that were significant across all densities included two reproductive parameters, *agemax* and *k*, and three female mortalities, mw_{AF}, $mw(0, F)$, and $ms(0, F)$.

At low and medium population densities, the remaining parameters sorted out in a fairly similar manner, with female mortality rates and several reproductive parameters having the strongest effects on growth rates (Table 5). The litter size of females bred as yearlings (l_1) was only important at the lowest density. The occupancy rate at which yearling breeding ceases ($oc_{max}(1)$) was only important at medium density.

At high density, a very different set of parameters was important, specifically the dispersal mortality related parameters. In addition, several *male* mortality rates were shown to be important predictors of growth rate (Table 5). At low and medium densities, it appears that there are few significant interactions between parameters, as evidenced by the fact that the 47 parameters, as main effects, explain 97% of the variation in growth rate (Table 4). This leaves a scant 3% to be explained by the myriad interaction terms or by non-linear relationships. This situation is different at high density, however, with only 75% of the variation in growth rate explained by these main effect terms. The remainder may be explained by interaction terms and by non-linear relationships.

The effect of litter size on growth rate, for the low and high population densities, is shown in Figure 16. The graphs indicate that the relationship between

Table 5. Summary of rankings of significant variables. The "Low-", "Medium-", and "High-density" columns show the composite rankings of the variables from those three sets of simulations. In each section, the parameters are ranked according to the sum of the ranks across the three densities. Blanks in the table indicate that the parameter did not have a significant effect on growth rate at that density.

	Description	Low	Medium	High
l_A	Adult litter size	1	1	1
agemax	Relative litter size parameter	3	2	10
mw_{AF}	Winter mortality, adult female	5	4	7
k	Relative litter size parameter	7	6	3.5
$mw(0, F)$	Winter mortality, kit female	2	3	13.5
$ms(0, F)$	Summer mortality, kit female	14	16.5	16
$mw(2, F)$	Winter mortality, 2-year female	6	5	
f	Female fraction at birth	8	8	
$b_{max}(1)$	Maximum fraction of yearlings that breed	4	13	
$mw(1, F)$	Winter mortality, yearling female	9.5	10	
$mw(3, F)$	Winter mortality, 3-year female	11	9	
$ms_{min}(2, F)$	Summer mortality, 2-year female	9.5	11.5	
$b_{max}(2)$	Maximum fraction of 2-year-olds that breed	12	11.5	
$b_{max}(3)$	Maximum fraction of 3-year-olds that breed	15	12	
ms_{AF}	Summer mortality, adult female	16.5	15	
l_1	Litter size of yearling breeders	13		
$oc_{max}(1)$	Occupancy rate at which yearling breeding reaches minimum		7	
$k_1(F)$	Female vulnerability parameter		14	
$ms_{min}(3, F)$	Summer mortality, 3-year female		18.5	
$oc_{min}(1)$	Occupancy rate at which yearling breeding begins to decline		18.5	
b_{disp}	Upper occupancy threshold for dispersal mortality effect			2
a_{disp}	Lower threshold for same			3.5
$mw(0, M)$	Winter mortality, kit male			5
$ms_{max}(2, M)$	Maximum dispersal mortality, 2-year male			6
mw_{AM}	Winter mortality, adult male			8.5
ms_{AM}	Summer mortality, adult male			8.5
$b_{min}(3)$	Minimum fraction of 3-year-olds that breed			11
$ms_{max}(3, M)$	Max. disp. mortality, 3-year male			12
$mw(1, M)$	Winter mortality, yearling male			13.5
$mw(2, M)$	Winter mortality, 2-year male			15

growth rate and litter size appears to be primarily linear. Tests of the quadratic effect of litter size are significant at all densities, but the amount of variation explained is two orders of magnitude smaller than the linear term.

5.3 Discussion

The most important uncertainty in the population model is the average litter size for adult females of the most fecund age class (l_A). This parameter, in conjunction with the relative reproductive rate equation (18), determines the litter size for all adult females. It is most important for two reasons: the growth rate is very sensitive to changes in this

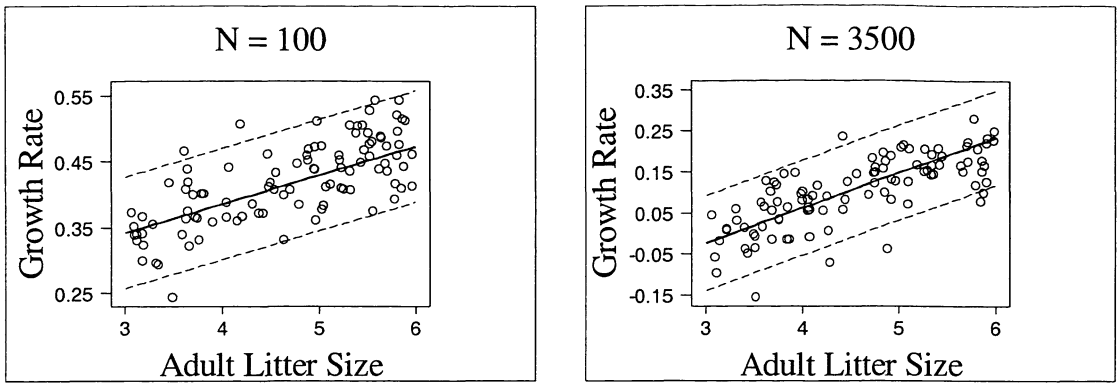

Figure 16. Growth rate as a function of adult litter size (l_A) at low and high population density. For the sake of clarity, only a random sample of 100 points (from the 2500 for each analysis) is plotted. The solid line is the simple linear regression fit to the entire data set. The dashed lines are 95% prediction bands, calculated *without* a multiple comparisons correction. Confidence bands are not shown because they are virtually indistinguishable from the fitted line on the scale of these graphs.

parameter; and there is considerable variability in this parameter, as measured by a large number of studies over the past half-century. The variability is most commonly attributed to habitat quality, with elevation and latitude also on the list of possible factors (Novak 1987a). Thus, for practical application of this (or any similar) beaver population model to a specific region, estimation of average litter size should be the highest priority, no matter what the density of the population.

Two reproductive parameters closely related to l_A, namely, k and *agemax*, should also be top priorities for estimation. The parameters control the relationship between average litter size and maternal age, and thus, through interaction with the age-distribution of females, can strongly affect the population growth rate across all densities. Estimation of these three parameters requires a study of litter size as a function of maternal age.

In addition, the natural mortality rates of kit and adult females are important determinants of population growth across all densities. There is some difficulty in measuring these rates, since the most common method of estimating age-related mortality is from the age-distribution of the harvest, which confounds natural and harvest mortality. The range of values mentioned for these parameters is huge, and these rates may vary regionally as well as temporally.

At high density, the population dynamics are much different than at low or medium densities. Two of the parameters that govern density-dependent dispersal mortality, a_{disp} and b_{disp}, have an effect on the growth of the population at high density, though not nearly the effect that litter size has. Estimation of these two parameters would require a careful study of dispersal mortality.

Estimation of the eight aforementioned parameters (Table 6), as well as an understanding of their temporal variability, would allow calibration of this population model for a particular region across the entire range of possible densities. Priorities for further refining the model would depend on the density of the population in question and the goals of

Table 6. Important parameters to estimate. This is just a condensed version of Table 5, with only the top three rankings shown for each density.

	Description	Low	Medium	High
l_A	Adult litter size	1	1	1
agemax	Relative litter size parameter	3	2	
k	Relative litter size parameter			3.5
$mw(0, F)$	Winter mortality, kit female	2	3	
b_{disp}	Upper occupancy threshold for dispersal mortality effect			2
a_{disp}	Lower threshold for same			3.5

management. In most cases where there is active beaver management, the goal is to maintain a "medium" population density, in which case, the results in Tables 4 and 5 can be used as a decision aid to guide research.

The sensitivity analysis shows that there is only *one* critical parameter and a small number of additional parameters that drive the dynamics of this model. This suggests that a refined version of the model, designed for practical use by beaver managers, should require explicit specification of the high priority parameters, but could condense the remaining parameters into a more simplified form.

6 Summary

I have presented a biologically-based, detailed population model for beaver that incorporates a great many of the dynamics that have been observed or suggested in past studies. It is my hope that its level of detail, its structure, and its parameter estimation motivate others to pursue a greater understanding of beaver population dynamics. I have shown that this model can be used to generate specific, testable hypotheses; that it can be used to identify research priorities; and that it can be used as a structure for synthesizing what is known about beaver population dynamics.

The structure of the model, specifically how density-dependent relationships have been handled, is certainly open to further evaluation, mainly because none of the density-dependent relationships suggested for beaver populations have ever been carefully documented. The high-density dispersal dynamics are the most speculative. Further, the dynamics of the model seem most complex at this density as well as most sensitive to small changes in the parameters. The only other population model I am aware of that addresses high-density dynamics in beaver is that of Molini et al. (1981)—between these two models, some very dramatic hypotheses are advanced. It is my conviction that where uncertainty about dynamics is large, these types of population models can provide guidance for research, whether it is pure research, or research tied to management.

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