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Spatial population dynamics of Microtus in grazed and ungrazed grasslands

Jonathan Peter Runge
The University of Montana

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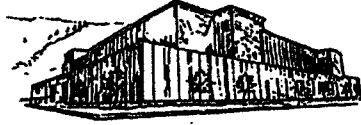
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8/98

SPATIAL POPULATION DYNAMICS OF *MICROTUS* IN GRAZED AND
UNGRAZED GRASSLANDS

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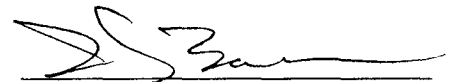
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Spatial population dynamics of *Microtus* in grazed and ungrazed grasslands

Graduate Committee Chair: I. Joseph Ball, Ph.D.

The field of spatial population dynamics has developed rapidly, especially in the realm of theory. One formulation of spatial population theory delineates sub-populations as either sources (sub-populations that provide a net gain to the overall population) or sinks (sub-populations that incur a net loss on the overall population). Many field studies have tested for the existence of source-sink dynamics but few have detailed how management actions may create sinks.

This study evaluates the effect of livestock grazing on populations of meadow vole (*Microtus pennsylvanicus*) and montane vole (*M. montanus*) in the Mission Valley of western Montana. Livestock grazing is a common management tool and economic resource in the western United States, but its effect on voles has been little researched. Voles are important members of their ecosystem because they form a large prey base and thus positively affect animal biodiversity, but they also exhibit high rates of granivory and herbivory and thus negatively affect plant biodiversity and agricultural economics.

Voles were trapped on four grids that were bisected by fences from 2002-2004. Vole populations in grazed areas experienced lower rates of apparent survival and per capita reproduction than vole populations in ungrazed habitats. Furthermore, net dispersal tended to flow from ungrazed to grazed habitat. These patterns supported the hypothesis of source-sink dynamics in vole populations.

Further analysis showed that the height and density of vegetation in grazed habitat showed a strong correlation with the apparent survival of voles. The pattern of decreasing rates of apparent survival corresponding with decreasing height and density of vegetation suggests that a reduction of the amount of vegetative cover on the landscape can affect population trajectories for voles.

Correspondingly, land managers may manipulate vole populations through livestock grazing to achieve specific management objectives. However, if extensive acreage is heavily grazed for long periods, the resulting reduction in vole abundance may adversely affect the abundance of the many animals that prey upon voles, potentially reducing animal biodiversity.

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Field technicians for this project included Eric O'Neil, Travis Shealy, Nami Bittner, Alex Bittner, John Head, Ryan Gann, Betsy Krier, and Jennifer Lovern. They all put in admirable effort in the face of tedious and odiferous field work.

The editing skills of Joe Ball improved this dissertation immeasurably; I shudder to think of the quality of this work without Joe Ball's input.

I give special thanks to my parents for advice and support and for introducing me to the natural world at a young age. My wife Kathy endured life as essentially a single mother for multiple days over the course of months during this project, a trial that cannot be underappreciated. My sons James and Nick have provided moments of light and discovery that obviated any stress induced by the world of academia. I look forward to returning the sense of discovery by introducing them to the natural world.

iii

Table of Contents

List of Tables

v

List of Figures

Chapter 1. The effect of livestock grazing on *Microtus* populations, an overview and introduction.

In this dissertation, I investigate the effect of livestock grazing on populations of meadow vole (*Microtus pennsylvanicus*) and montane vole (*M. montanus*) in the Mission Valley of western Montana. The overarching hypothesis of the study is that livestock grazing induces spatial structure in vole populations by reducing survival and reproduction.

Subsidiary hypotheses are based upon four possible types of spatial structure induced by grazing. Source-sink dynamics occur when mortality exceeds natality in sub-optimal ("sink") habitat, the reverse is true in optimal ("source habitat"), and dispersal generally flows from source to sink (Holt 1984, Pulliam 1988). Balanced dispersal dynamics occur when natality exceeds mortality in both optimal and sub-optimal habitat, and the number of individuals dispersing between habitats is equal (McPeek and Holt 1992). Unbalanced dispersal dynamics occur when natality exceeds mortality in both habitats, but dispersal generally flows from sub-optimal to optimal habitat (Lin and Batzli 2001). Reciprocating dispersal dynamics occur when dispersal varies according to the density of organisms in optimal habitat (Morris et al. 2004). Thus, in populations with varying density, reciprocating dispersal can incorporate the dispersal patterns of source-sink, balanced, and unbalanced dispersal dynamics.

Both conceptual and empirical aspects of the study present unique challenges. Foremost is that sources and sinks have been defined differently by different researchers (e.g., Holt 1984, Roughgarden and Iwasa 1985, Pulliam 1988, Donovan et al. 1995, Doncaster et al. 1997). Much of the inference regarding sources and sinks has been

1

extended to conservation settings in which sources are considered high-quality habitat and sinks low-quality. However, many researchers have failed to consider emigration when delineating sources and sinks, potentially leading to the situation in which a habitat that produces and exports many individuals is labeled a sink (e.g., Donovan et al. 1995, Perkins et al. 2003). In Chapter 1, I review some of the methods for delineating sources and sinks and present a method for doing so that incorporates emigration.

Montane and meadow voles are sibling species (Murie 1971, Douglass 1976a), i.e., they co-occur and exhibit similar external features (Futuyma 1998). The two species can be differentiated by examining dental patterns, but this method is difficult to use on live specimens. A quick and efficient method for identifying live individuals to species was unknown prior to the initiation of this study (K. Foresman, personal communication). During the first week of field research, I noted that a subset of voles tended to exhibit lighter coloration with silver-tipped guard hairs, while a separate subset tended to exhibit darker coloration with the tips of guard hairs exhibiting a reddish color. Based upon these characteristics, I began assigning a tentative species classification to each individual with the lighter colored individuals receiving a classification of "montane vole" and the darker individuals receiving a classification of "meadow vole." During the three years of the study, 293 individuals receiving a tentative species classification died in traps and were later identified to species; 268 (91.5%) of these received a correct species classification. During the final field season, 66 of 68 (97.1%) individuals that died in traps and were identified to species received correct species classifications, suggesting the two species can be reliably differentiated in the field. Chapter 2 summarizes the

2

different factors that may influence the probabilities of correct classification for the two species.

Misclassifying individuals can lead to bias in estimates of survival and dispersal (Kendall et al. 2003, Nichols et al. 2004). To account for individuals that were never identified to species, I formulate a novel statistical model that incorporates incorrect assignment of individuals to species while allowing for accurate estimation of survival and movement. This model and a corresponding example are detailed in Chapter 3.

In Chapter 4, I integrate work from the previous chapters to investigate the manner in which livestock grazing affects vole populations. Specifically, I estimate vital rates with methodology introduced in Chapter 3 and use these estimates to derive the metric introduced in Chapter 1 that can be used to categorize habitat quality. For meadow voles, livestock grazing appeared to induce a structure of sources and sinks. For montane voles, livestock grazing most likely induced a similar structure, but the amount of vegetation removed affected whether grazed habitat was designated a source or sink. If intervals between grazing events are of sufficient length, then rates of apparent survival may increase with grass height and density, suggesting that land mangers can influence spatial structure in populations of montane voles solely by controlling livestock access to grasslands.

3

Chapter 2. The role of local populations within a landscape context: defining and classifying sources and sinks

Abstract: The interaction of local populations has been the focus of an increasing number of studies in the past 30 years. The study of source-sink dynamics, especially, has generated much interest. When investigating how local populations interact, emigration from the focal population is an important process, especially for local populations that rely on immigration for persistence yet export many individuals. Here, we review theoretical criteria used to differentiate sources and sinks and expand upon a criterion (denoted "contribution" or C^r) that incorporates successful emigration in differentiating sources and sinks but that makes no restrictive assumptions about dispersal or equilibrium processes in populations of interest. C^r is rooted in the theory of matrix population models, yet also contains clearly specified parameters that have been estimated in previous empirical research. Thus, C^r integrates theory and empiricism. We additionally review much of the empirical work conducted between 1981 and 2001 regarding source-sink dynamics. Of 138 published articles attempting to differentiate sources and sinks, only 13 contained estimates of emigration, local recruitment, and apparent survival. We suggest that estimates of emigration are important for delineating sources and sinks and, more generally, for evaluating how local populations interact. This suggestion has direct implications for issues such as species conservation and habitat management.

Key words: source-sink, habitat quality, emigration, immigration, apparent survival, local recruitment

Introduction

Local populations profoundly affect the viability of metapopulations, and understanding the roles local populations play in metapopulations is an area of increasing focus for both ecologists and resource managers. One conceptual classification of such roles distinguishes "sources" and "sinks" based on patterns of birth, death, immigration, and emigration (Holt 1984, Pulliam 1988). Source-sink dynamics have entered theoretical discussions of population and evolutionary ecology, and consequently have become the focus of numerous empirical studies. Despite searches for definitive evidence of sources and sinks (e.g., Dias 1996, Pulliam 1996), examples have been difficult to find (Diffendorfer 1998), perhaps because the estimation methods and the theory have not been integrated.

The general intuition for defining sources and sinks is widely appealing: source-sink population dynamics arise when dispersal connects at least two populations, and individuals emigrating from one population (a source) support another (a sink). A source must be self-supporting; that is, reproduction must outweigh mortality (Holt 1984, Shmida and Ellner 1984). The reverse is true in a sink, where mortality outweighs reproduction. The source-sink concept was introduced in the form of "dispersal sinks" (Lidicker 1975), then modified to include "donor" and "receptor" habitats (Hansson 1977), and, finally, investigated mathematically (Holt 1984, 1985, Shmida and Ellner 1984, Roughgarden and Iwasa 1986, Pulliam 1988). The concept became exceedingly popular, and the number of published papers explicitly investigating some aspect of source-sink dynamics rose dramatically in the late 1990s and early 2000s (fig. 1).

5

The rise in popularity of source-sink dynamics has occurred in both theoretical and empirical realms of biology. Accurate classification of local populations (or habitats or sites) as sources or sinks, and identification of their relative contributions to the larger population of interest, has become important to empirical biologists (fig. 2) and the resource managers who rely upon their research. For instance, managers may wish to conserve source but not sink habitats when faced with decisions regarding habitat management (Crowder et al. 2000, Semlitsch 2000). In such situations, identifying which area is a source and which is a sink is crucial. Thus, accurate estimation of the relative contributions of local populations in different habitats to systems of interest is important in an increasingly fragmented natural world.

Unfortunately, a gap exists between existing theory and the ability to estimate source-sink dynamics in natural populations. For example, many empirical studies of vertebrates use mark-recapture techniques to estimate vital rates. Mark-recapture techniques generally enable the estimation of so-called 'apparent survival,' the probability of surviving and staying within a local population. When only estimates of reproduction and apparent survival are used to describe habitat quality, then all animals that disappear from the study area are assumed to be mortalities when in reality some may be emigrants. This leads to a bias in how we quantify habitat quality: areas that export many individuals may be seen as sinks because emigrants are tallied as mortalities. Therefore a valuable addition to source-sink theory would be a criterion that explicitly incorporates the relevant rate parameters (reproduction, survival, and emigration) and thus rigorously quantifies the contributions that a local population makes to the larger metapopulation. (We define a metapopulation as a system of interbreeding individuals

6

that encompasses two or more habitats or locations, while noting that alternate definitions of the term exist [Hanski and Simberloff 1997].)

An additional concern is that both spatial and temporal extent of sampling can influence how we view source-sink dynamics. As the size of a study area increases, dispersing individuals become less likely to disappear from a study and estimates of survival and emigration become less biased (Martin et al. 1995, Cilimburg et al. 2002). Conversely, sampling at scales that are small relative to a species' dispersal tendencies leads to a bias in classifying sources as sinks. Increasing temporal extent allows for the investigation of how environmental stochasticity and density-dependence may affect the classification of sources and sinks. Studies conducted over short time periods may miss fluctuations in population processes that would cause a population to be classified as a source one year and a sink the next (Stacey and Taper 1992, Thomas et al. 1996, Boughton 1999).

Here we review some of the theoretical and much of the empirical literature concerned with the classification of source-sink dynamics. Beginning with theory, we review the Pulliam (1988) model and other criteria used to differentiate sources and sinks, expand upon a single preferred criterion that incorporates emigration into source-sink classification, and present additional criteria that could be used to evaluate the contributions of local populations to metapopulations. Turning to empirical applications, we review the methods used previously to classify sources and sinks, and describe how estimation in the field needs to be tied to theory.

7

Describing the Role of a Local Population within a Landscape

Defining Sources and Sinks

Many theoretical depictions of source-sink dynamics exist (e.g., Holt 1984, Shmida and Ellner 1984, Roughgarden and Iwasa 1986, Pulliam 1988, Davis and Howe 1992). Because Pulliam's (1988) model offers perhaps the most accessible characterization of criteria regarding sources and sinks, we review that particular model, and then compare criteria of other theoretical works.

In his landmark paper, Pulliam (1988) first defined sources and sinks in terms of birth, immigration, death, and emigration (BIDE model, e.g., Cohen 1969). Pulliam (1988) considered a spatially distributed population with m subpopulations occupying discrete habitats or compartments. The system of subpopulations was then characterized by the set of location-specific numbers of births (b_j for location j), deaths (d_j), immigrants to location j from all other locations (i_j) and emigrants from location j to all other locations (e_j). The entire system is in dynamic equilibrium when the number of animals in each subpopulation, n_j, is constant over time (or if n_j is viewed as a random variable, when $E(n_j)$ is a constant). Such a dynamic equilibrium occurs when

$b_j + i_j - d_j - e_j = 0$, i.e., when gains to each subpopulation equal losses.

Given the above development, Pulliam (1988) defined a source compartment or location as one for which

$$b_j > d_j \text{ and } e_j > i_j, \tag{1}$$

and a sink compartment as one for which

$$b_j < d_j \text{ and } e_j < i_j. \tag{2}$$

Pulliam (1988) noted that these definitions applied only to populations at equilibrium (i.e., unchanging abundance over time) and suggested that more general definitions of a source and sink, respectively, were a subpopulation that, over a relatively long time period (e.g., several generations), shows no change in population size and is a net exporter or net importer of individuals.

After defining sources and sinks using the BIDE model, Pulliam shifted focus to habitat-specific demography and classified habitats according to the metric

$$\lambda = P_A + P_J \beta \tag{3}$$

where P_A and P_J are the habitat-specific survival probabilities for adults and young from the initiation of breeding season until just before pre-breeding emigration and β is the habitat-specific per capita reproductive rate. Pulliam (1988:655) considered a habitat a source if $\lambda > 1$ and a sink if $\lambda < 1$, thus basing source-sink classification solely on within-habitat birth and death rates (note that $\lambda > 1$ is equivalent to $b_j > d_j$; the second condition of eq. [1], $e_j > i_j$, is necessarily true if the first condition holds and the population is at equilibrium).

The classification of habitats using λ is certainly sensible within the context of Pulliam's model but has led to some confusion in real-world applications of source-sink theory. In particular, Pulliam's definition of the P's did not include mortality during emigration. Such mortality, however, can certainly influence the true contribution of dispersers from a focal location to the growth of the metapopulation. In the extreme, we could imagine a local population classified as a source by equation (3) but which contributed no individuals to other populations because of 100% mortality during dispersal. Thus, actual applications of source-sink theory would be most accurate when

9

survival and subsequent recruitment of emigrants into other components of the metapopulation are estimated.

Past definitions of sources and sinks are not consistent. Several theoretical works have presented criteria for differentiating sources and sinks that, like Pulliam's λ, do not include a term for emigration (e.g., Shmida and Ellner 1984, Davis and Howe 1992). However, other theoretical works have included emigration in criteria (e.g., Roughgarden and Iwasa 1986, Doncaster et al. 1997) or, at least, considered emigration as part of the conceptual definition of sources and sinks (e.g., Diffendorfer 1998). Perhaps the key issue lies in defining a sink. Holt (1984:390) defined a sink as a local population "maintained solely by immigration." However, Diffendorfer (1998: 419-420) stated that "the best method for testing the assumption concerning the existence of sinks...[is]...experimentally eliminating dispersal and determining if populations...decline to extinction." These two approaches are not equivalent. The first does not consider the process of emigration; a population that exports many individuals may still be supported by immigration. The second approach does incorporate emigration; if dispersal is eliminated, then all potential emigrants would stay in and thus contribute to the persistence of the local population. Although the second approach confounds emigrant and resident survival, it is conceptually preferable because it tallies emigrants as gains rather than losses, an approach that better quantifies the contributions a local population offers to the metapopulation.

The Contribution of a Local Population

We propose a criterion for distinguishing sources and sinks that includes both survival and emigration rates of adults and juveniles over an entire breeding cycle (thus it

10

includes mortality during emigration). First we define ϕ_a^{rs} as the probability that an animal in subpopulation r in a particular year (or breeding period) is alive and in subpopulation s the next year (or breeding period), where a denotes age (J = juvenile, A = adult) and r and s denote locations, with $s \neq r$ indicating movement from focal subpopulation r to another subpopulation s, and with $s=r$ indicating retention in the focal subpopulation r. For example, ϕ_J^{rr} is the probability that a juvenile survives and remains in subpopulation r.

Given these definitions, we can write the contribution of a focal subpopulation (r) to the system of interest as:

$$C^r = \phi_A^{rr} + \sum_{s \neq r} \phi_A^{rs} + \beta^r (\phi_J^{rr} + \sum_{s \neq r} \phi_J^{rs}),$$
(4)

where β is the reproductive rate (juveniles per adult) in the focal subpopulation. C^r is the per capita contribution of the focal subpopulation to the metapopulation: for each individual in subpopulation r at time t, there will be C^r individuals in the metapopulation at time $t+1$. Note that if we introduce a new "true survival" term, S^r, to denote survival of both residents and emigrants originating in the focal population (e.g., $S_A^r = \phi_A^{rr} + \sum_{s \neq r} \phi_A^{rs}$),

then the criterion $S_A^r + S_J^r \beta^r$ is identical to C^r (see McGowan and Otis 1998).

If the term "source" is to reflect the contribution of the focal location to metapopulation growth, then equation (4) may be preferred to equation (3). If $C^r > 1$, then the focal subpopulation contributes more individuals than it loses via mortality and is a source. If $C^r < 1$, the focal subpopulation loses more animals to mortality than it contributes and is a sink. By explicitly incorporating emigration processes in the criterion (the ϕ^{rs} parameters include survival and movement), we emphasize the

11

importance of emigration for classifying sources and sinks. Roughgarden and Iwasa (1986) and Doncaster et al. (1997) used similar metrics to classify sources and sinks but did not investigate how differences between these metrics and other criteria (e.g., Holt 1984, Shmida and Ellner 1984, Pulliam 1988, Davis and Howe 1992, Donovan et al. 1995) affected source-sink classification.

Multiple stage or age-classes. If the species of interest takes more than one time unit (i.e., year) to reach breeding age, or if the research design requires post- or intermediate birth pulse sampling, then C^r must be modified to incorporate stage (or age) structure. Doing so requires three steps. First, let each stage within a site have its own contribution metric. Second, weight the contribution metrics for the stages within a site by their current or stable stage distributions. Third, sum the weighted, stage-specific contribution metrics within each site to calculate C^r (Appendix A). Interest in short-term dynamics would suggest using the current stage distribution for the weights, interest in long-term dynamics, the stable stage distribution (from, say, eigenanalysis of the multistate transition matrix). Comparing C^r obtained by both methods may be useful. For instance, if recent disturbance has resulted in a year of decreased reproduction and/or juvenile survival (e.g., Jones et al. 2001), then *in situ* recruitment in subsequent years may be low enough to cause the local population to be a sink. However, long-term dynamics best described with the stable stage distribution may suggest that the local population of interest has the potential to be a source. The inverse situation may occur if a banner year for reproduction occurs in a local population that usually is a sink. Thus, contrasting C^r obtained from both the current and stable stage distributions may highlight important differences between short- and long-term dynamics in the local population of interest.

12

Additional Descriptors of the Role of a Local Population

Many theoretical and empirical works have used estimates of apparent survival (ϕ), the probability of an individual surviving and staying within the population of interest, to differentiate sources and sinks (e.g., Shmida and Ellner 1984, Davis and Howe 1992, Donovan et al. 1995, Perkins et al. 2003). We denote the metric

$$R^r = \phi_A^{rr} + \beta^r \phi_J^{rr} \tag{5}$$

as the "self-recruitment rate" for local population r, which represents the ability of a local population to maintain itself through retention and self-recruitment. The self-recruitment rate (R^r) is not equivalent to the contribution (C^r), but they are related:

$$\begin{aligned} C^r &= \phi_A^{rr} + \phi_A^{rs} + \beta^r(\phi_J^{rr} + \phi_J^{rs}) \\ &= (\phi_A^{rr} + \beta^r \phi_J^{rr}) + (\phi_A^{rs} + \beta^r \phi_J^{rs}) \\ &= R^r + E^r, \end{aligned} \tag{6}$$

where E^r (emigration) measures the ability of a local population to contribute individuals to other local populations. R^r incorporates 3 of the 4 vital rates that influence numbers of animals in an area of interest: reproduction, mortality and emigration (although mortality and emigration are confounded in the sense that they both constitute losses to the local population). Thus, R^r reflects an asymmetric treatment of movement processes, in that it incorporates all losses from the focal population (including emigration) but not all gains (immigration is not included). Indeed, this asymmetry characterizes many population-modeling exercises based on estimates of vital rates obtained in field studies (e.g., Nichols et al. 2000, Franklin et al. 2004). We believe C^r is preferable to R^r because it includes the contribution of local population r to the other components of the metapopulation. Use of R^r to classify local populations may result in those populations with high emigration rates being labeled sinks when they are actually *sources* of

13

individuals for other populations (although any local population identified as a source by R^r will also be identified as a source by C^r).

Contrasting R^r and C^r is useful because it provides additional detail for understanding the role a local population plays in a larger context. R^r is necessarily less than or equal to C^r; therefore, it is possible that $C^r > 1$, yet $R^r < 1$. That is, a local population can be a net contributor to a metapopulation, yet not retain enough individuals to support itself (thus requiring immigrants for persistence). This classification has been labeled a "dependent source" (Hixon et al. 2002) and may be common. Migratory songbirds and ducks, such as *Dendroica caerulescens* (black-throated blue warbler) (Sillett and Holmes 2002) and *Anas clypeata* (northern shoveler) (Blums et al. 2003), exhibit low fidelity to natal areas. In nonmigratory species as well, e.g., *Strix occidentalis occidentalis* (California spotted owls) (Franklin et al. 2004), most hatch-year birds may disperse from natal areas. Thus even the best habitats may depend on immigrants to form the adult population yet still provide many emigrants to other habitats. This highlights an important conceptual difference between R^r and C^r. If we define sinks with R^r, then species with high emigration rates could persist with all local populations being categorized as sinks. If we define sinks with C^r, then a species must be supported by at least one local population that is a source. If the source-sink paradigm is to be used for habitat management, with source populations indicative of "good habitat" and sink populations indicative of "bad habitat", then C^r may be the more appropriate criterion because it differentiates those populations that represent net gains for the system of interest from those that represent net losses.

14

Most treatments of source-sink distinctions (e.g., Pulliam 1988 and many others) assume that populations are in dynamic equilibrium, that is, abundances in local and metapopulations are constant (or at least the expectations of local and metapopulation abundance do not change). However, many investigations of source-sink dynamics may apply to populations that have undergone anthropogenic disturbance and may not be in dynamic equilibrium. Therefore, one additional metric may be useful in describing natural systems, the growth rate of a local population,

$$\lambda_{loc}^r = \frac{N_{t+1}^r}{N_t^r} = R_t^r + I^r,\tag{7}$$

where N_t^r is the local abundance at time t, and I^r is a per capita measure of immigration (i.e., the number of new immigrants present in the local population at time $t+1$ divided by the abundance at t). At equilibrium, $\lambda_{loc}^r = 1$ for all r. Note that

$$\lambda_{loc}^r = C^r - E^r + I^r,\tag{8}$$

thus if I^r and E^r are known to be equal, as in the case of balanced dispersal (McPeek and Holt 1992) or populations closed to dispersal (e.g. Gagen et al. 1998), then $\lambda_{loc}^r = C^r$.

At least one conceptual work has classified sources and sinks based solely on whether populations export individuals (Hixon et al. 2002). Indeed, Hixon et al. (2002) provide useful terminology for five different types of local populations connected by dispersal, emphasizing the inability to adequately describe components of such systems in terms of the original source-sink description. Rather than review the terminology of Hixon et al. (2002), we simply note that precise descriptors of these types of local populations can be developed using the three metrics (C^r, R^r, and λ_{loc}^r) and two dispersal processes (E^r and I^r) described above.

15

The Relationship between C^r and Metapopulation Growth Rate

C^r has a theoretical connection to the asymptotic growth rate of the metapopulation (λ_m). If we define a set of m sub-populations that have rates of self-recruitment and retention, R^r ($r = 1$ to m), and that are linked by dispersal processes with per capita dispersal rates, E^{rs}, from sub-population r to sub-population s ($r, s = 1$ to m, $r \neq s$), then the dynamics of this metapopulation can be described by a transition matrix

$$
A = \begin{bmatrix}
R^1 & E^{21} & E^{31} & \cdots & E^{m1} \\
E^{12} & R^2 & E^{32} & \cdots & E^{m2} \\
E^{13} & E^{23} & R^3 & \cdots & E^{m3} \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
E^{1m} & E^{2m} & E^{3m} & \cdots & R^m
\end{bmatrix}
\tag{9}
$$

with one-time-step changes given by

$$
n_{t+1} = An_t
\tag{10}
$$

where n_t is a column vector of length m containing the sizes of each sub-population at time t. Next, we define the per capita contribution from sub-population r with equation (6) and note that these contributions are the column sums of A, that is,

$$
1'A = \begin{bmatrix} C^1 & C^2 & C^3 & \cdots & C^m \end{bmatrix} = C'.
\tag{11}
$$

Let λ_m be the dominant eigenvalue and w be the corresponding right eigenvector of A. Then, by definition of an eigenvalue, $Aw = \lambda_m w$ and when both sides are multiplied by a row vector of 1's,

$$
1'Aw = 1'\lambda_m w.
\tag{12}
$$

Equation (11) can be substituted into the left hand side of equation (12) and λ_m (a scalar) can be factored out of the right hand side of equation (12), resulting in $C'w = \lambda_m 1'w$. By matrix multiplication,

16

$$\sum_{r=1}^{m} C^{r} w^{r} = \lambda_{m}.$$ (13)

Thus the sum of the contributions, weighted by the stable site distribution, is the overall asymptotic growth rate of the metapopulation. Intuitively, this makes sense: C^{r} is the per capita contribution of patch r to the metapopulation, and the average of the m contributions, weighted by the relative population size in each patch, will be the per capita contribution of the entire metapopulation to itself in the next time step, i.e., the growth rate. This points to the general usefulness of the C^{r} metric: even in non-spatial, stage-structured matrices, C^{r} can be used to analyze the relative importance of each stage class to the population as a whole.

Additional Criteria: Reproductive Value and Seniority

A second metric that quantifies the relative value of different local populations is the multiple-location analog of Fisher's (1930) reproductive value (Willekens and Rogers 1978, Lebreton 1996, Nichols 1996, Rousset 1999a). Reproductive value (v^{r}) is the relative contribution of an individual in a local population to the size of the whole population in the distant future (e.g., Mertz 1971) and can be calculated analytically for matrix models (Caswell 2001) as the left eigenvector corresponding to the dominant eigenvalue of a transition matrix like equation (9). By comparing reproductive values, we can compare local populations inhabiting different patches (or habitats) in terms of their relative contribution to the long-term growth of the metapopulation. When the reproductive value vector for patch r is normalized so that $\sum_{r} w^{r} v^{r} = 1$, the criterion $v^{r} >$ 1 identifies patches that contribute to future generations in greater proportion than their numbers (Rousset 1999a, Kawecki 2004). How does v^{r} compare to C^{r}? First, v^{r}

17

integrates fitness over the lifetime of an individual and contribution into the distant

future, whereas C^r measures fitness and contribution over one time-step. Second, at

equilibrium, v^r and C^r produce equivalent classifications of sources and sinks in two-

population systems, but not in systems with more than two local populations; the habitat

to which animals emigrate can be more important than the number of animals emigrating,

because individuals that emigrate to good quality habitat will have a longer legacy than

individuals that emigrate to poor quality habitat (Kawecki 2004). Third, calculation of v^r

requires estimates of the pertinent life-history parameters ($\beta^r, \phi_J^{rr}, \phi_J^{rs}, \phi_A^{rr}, \phi_A^{rs}$) within

and among all patches in the population, whereas C^r can be calculated from knowledge of

only one local site (if that knowledge includes information on survival during

emigration). In cases when the information needed to parameterize a multi-patch matrix

model (and hence, estimate v^r) is available, that information is also sufficient to calculate

C^r, and researchers could present both metrics for local populations of interest, thus

providing a more complete description of the short- and long-term roles local populations

play within the metapopulation.

A third metric that can quantify the relative value of different local populations is

seniority, which is computed using reverse-time, mark-recapture methodology (Pollock et

al. 1974, Pradel 1996, Nichols et al. 2000). The seniority parameters of reverse-time

monitoring focus on the population growth rate of adults of a particular local population

and assess the contributions of adults and young from the same and other local

populations to this growth rate. So, unlike C^r, seniority provides a metric that assesses

contributions to, rather than from, a particular local population. Like C^r, seniority

parameters from specific local populations need to be weighted by local population

18

abundances (N^r), in which case seniority parameters can be used to assess contributions of different local populations to overall growth of the entire system (Appendix A). Although estimating N^r may reduce the practical utility of this approach to estimating contributions, we provide this information as a reminder that both forward- and reverse-time estimators deal with the same demographic process, and the two methods yield consistent results.

We do not review four additional metrics that use patch occupancy data to assess the contributions a local population makes to a metapopulation (Ovaskainen and Hanski 2003). These metrics are valuable tools for management and conservation when colonization-extinction dynamics occur (Frank 2005), but because colonization-extinction processes appear to be a rather specific form of metapopulation dynamics (Harrison and Taylor 1997), we focus on the more general metrics presented above.

Review of Empirical Methods

The challenge of empirical studies is to make a careful link between relevant ecological theory and estimation methods used in the field. The ecological theory above suggests that separating both immigration from *in situ* reproduction and permanent emigration from mortality is necessary to evaluate the role of a local population within the larger population spread across the landscape. In most ecological studies, however, differentiating estimates of loss and gain into those components is problematic. For example, capture-recapture survival estimates correspond to the probability that an individual alive in the area of interest in period t is still alive and in the area (not a permanent emigrant) in period $t+1$. The complement of a capture-recapture survival estimate thus confounds death and permanent emigration (e.g., Lebreton et al. 1992,

19

Williams et al. 2002). Capture-recapture estimates of gains to a population (e.g., the Jolly-Seber B_i; Jolly 1965) confound gains from both *in situ* reproduction and immigration. Many studies of population dynamics commonly focus solely on reproduction (e.g., litter size, clutch size, fledglings per nest) and make no attempt to estimate immigration. These approaches fail to provide separate estimates of recruitment arising from *in situ* reproduction and immigration.

To investigate existing empirical methodology used for differentiating sources and sinks, we conducted a search in the Biological Abstracts and Wildlife Worldwide on-line databases on the terms "dispersal sink(s)," "source (or sink) habitat(s)," "source (or sink) population(s)," "mortality sink(s)," and "source-sink." Articles obtained in this original search contained citations to articles explicitly examining source-sink dynamics that the original search did not encompass, and we included these in our analysis. We constrained our search to the years 1975—2001 because the "dispersal sink" concept was introduced in 1975 (Lidicker 1975), and both on-line databases were still updating articles for 2002 when the search was conducted. We found 283 articles explicitly investigating source-sink dynamics, 138 of which empirically attempted to identify the existence of source-sink dynamics for vertebrate populations. Ninety-eight studies (71%) used parameter combinations unable to distinguish sources from sinks, 31 (22%) used R^r to distinguish sources from sinks, and nine (7%) calculated C^r or a similar metric. The review below is cursory; a full analysis of all 138 studies can be found in Appendix B.

Parameters Insufficient to Differentiate Sources and Sinks

Thirty-one different parameter combinations were used that involved assumptions too stringent to differentiate sources from sinks. We do not review all 31 of these

20

methods but instead concentrate on those that are most commonly used or that represent the latest developments in technology and theory.

Twenty-four studies (17%) attempted to identify sources and sinks by estimating only abundance (N), basing this identification on the assumption that abundant populations must be sources and small populations must be sinks (e.g., Peres 2001). However, failure to identify which primary population processes (birth, death, immigration, or emigration) drive changes in abundance often leads to incorrect inferences about the status of local populations with high abundance (Van Horne 1983, Williams et al. 2002). Theoretically, low abundance sources can support high abundance sinks through dispersal (Pulliam 1988). Thus, empirical classification of source and sink could be reversed from true classification if N is used as the sole criterion for classification.

Thirty-three studies (24%) used either survival or reproduction, sometimes in combination with abundance, to identify sources and sinks. The rationale behind using only birth rate (β^r) is that it is the main process driving local population dynamics (e.g., Hoover et al. 1995). This approach seems to be common in migratory bird studies with the following assumptions: adult survival during the nesting season is 1.0, and overwinter survival is unrelated to the habitat in which an individual nested the previous breeding season. Such an approach enables evaluation of habitats relative to breeding production but does not allow the delineation of sources and sinks because it ignores a crucial component of population ecology: the per capita number of juveniles that survive to breeding age and stay in the system of interest. Thus, using β^r as the sole parameter defining source-sink systems can be misleading. Additionally, estimating only β^r or ϕ_j^{rr}

21

ignores the process of immigration. To differentiate immigrants from local recruits that were born into the population of interest, estimates of both β^r and ϕ_J^{rr} are necessary. This underlines the importance of separately estimating local recruitment ($\beta^r \phi_J^{rr}$) and immigration in any study investigating local population dynamics (Connor et al. 1983, Nichols and Pollock 1990, Anders et al. 1997, Nichols et al. 2000). Immigrants are products of a different local population, and if immigrants are tallied as local recruits, sinks may be misclassified as sources. The rationale behind the addition of N^r or λ_{loc}^r to the parameter combinations above is that these metrics provide additional evidence regarding habitat quality, an assumption that is not necessarily true (Van Horne 1983, Pulliam 1988). Studies concentrating solely on adult survival assumed that areas with lower adult survival must be sinks (e.g., Knight et al. 1988, Cunningham et al. 2001). This assumption is erroneous because fecundity certainly affects which areas may be sources and sinks. Estimating β^r and ϕ_A^{rr} does not enable full investigation of local population dynamics because, as noted above, an estimate of $\beta^r \phi_J^{rr}$ is necessary for evaluating the relative effects of immigration in a local population and survival processes for juveniles can strongly affect local population dynamics (Anders et al. 1997).

Seven studies (5%) attempted to identify source-sink dynamics using only information on presence/absence (P/A). One rationale behind using P/A is that a population must be a sink if it goes extinct (e.g., Celada et al. 1994). The transition from presence to absence indicates that all individuals died or emigrated; therefore $R^r = 0$, and the population could be considered a sink if R^r is used as a criterion. However, if emigration rather than mortality causes the presence-absence transition, then the focal population would be a source of individuals for other populations. For instance,

22

extinctions of *Microtus agrestis* (field vole) populations on small islands in the Baltic Sea appear to be driven more by emigration than by mortality (Crone et al. 2001). As mentioned above, recent theoretical work has shown that *P/A* data can be used to estimate the contributions of a local population to a classical colonization-extinction metapopulation (Ovaskainen and Hanski 2003). Nevertheless, "presence" of individuals at a location provides little information about source-sink dynamics, because extant local populations can be either sources or sinks. Thus, use of *P/A* data may not be appropriate for differentiating sources and sinks (Doak and Mills 1994, Clinchy et al. 2002).

Five studies (4%) used combinations of emigration, immigration, and *N* in an attempt to classify sources and sinks, perhaps under the view that dispersal information alone defines sources and sinks (i.e., Hixon et al. 2002). This view is supported only if the system is at equilibrium (i.e., $\lambda^r_{loc} = 0$), which none of the five studies demonstrated.

Four studies (3%) attempted to differentiate sources and sinks using genetic data. All four studies assumed a population genetic model in which the F_{st} metric should show either increased differentiation among purported sink populations, or more migration between sources and sinks than among sinks or among sources (e.g., Dias et al. 1996). However, both population differentiation and estimates of dispersal derived from F_{st} appear to be inaccurate in source-sink systems (Rousset 1999b, Whitlock and McCaughly 1999). Although isolation by distance methods provide accurate estimates of dispersal that are robust to some forms of spatial and temporal heterogeneity in demographic parameters (Sumner et al. 2001, Leblois et al. 2004), they cannot reliably differentiate sources and sinks (Rousset 1999b). Perhaps future efforts involving assignment tests (Paetku et al. 1995, Rannala and Mountain 1997) of samples obtained from all local

23

populations in the system of interest will generate reliable estimates of dispersal in source-sink systems, which could then be used with estimates of $\beta^r \phi_J^{rr}$ and ϕ_A^{rr} to differentiate sources and sinks.

Use of R^r

Many theoretical studies have used R^r as a criterion for differentiating sources and sinks (e.g., Shmida and Ellner 1984, Davis and Howe 1992), and 11 empirical studies (8%) have followed suit by calculating R^r from demographic processes estimated in the system of interest (e.g., Saether et al. 1999, Geertsma et al 2000, Zanette 2000). (We note that an additional twenty studies [14%] calculated R^r either by simulating values for unknown parameters or by using values estimated in other systems.) All 11 suggested the existence of sinks as defined by R^r, but defining sinks with R^r may not provide accurate information in terms of local population or habitat quality if focal species exhibit high emigration rates. If we define sinks with R^r, then species with high emigration rates could possibly persist in systems composed entirely of sinks. If only sink populations are found in systems of interest, then "sink-sink", rather than source-sink, dynamics may occur, a situation that may transpire frequently given some of the high rates of dispersal observed in nature (e.g., Sinsch 1997, Gaona et al. 1998, Hobson et al. 2004).

Studies Estimating C^r

Nine studies (7%) calculated C^r (or a similar metric), and eight of these found at least one sink in the system of interest. An overarching question regarding sinks is: Are they caused by natural habitat quality (Holt 1993) or by "anthropogenic risks" (Doak 1995)? Of the eight studies that identified sinks, six cited possible causes related to human-induced mortality. For instance, handling effects of researchers on common

24

bushtail possum (*Trichosurus vulpecula*) (Clinchy et al. 2001), and illegal killing of hen harrier (*Circus cyaneus*) (Etheridge et al. 1997), Iberian lynx (*Lynx pardinus*) (Gaona et al. 1998), and grizzly bear (*Ursus arctos horribilis*) (Mace and Waller 1998) were shown to induce source-sink dynamics. Additionally, legal harvest may have resulted in the formation of a sink population for mourning doves (*Zenaida macroura*) (McGowan and Otis 1998), and anthropogenic dewatering of streams may have caused source-sink, colonization-extinction dynamics in Ouachita madtom (*Notorus lachneri*) (Gagen et al. 1998). Conversely, naturally occurring density-dependent dispersal to sub-optimal habitat may have induced source-sink structure in a population of Spanish imperial eagles (*Aquila adalberti*) (Ferrer and Donazar 1996). Balanced dispersal, rather than source-sink, dynamics occurred in two situations: experimental manipulation of food and cover in populations of meadow and prairie vole (*Microtus pennsylvanicus* and *M. ochrogaster*) (Lin and Batzli 2001), and nest box-associated population dynamics of collared flycatcher (*Ficedula albicollis*) (Doncaster et al. 1997). Although the latter study quantified four sink populations, the authors theorized that if they had measured emigration from the studied metapopulation, then all local populations would have been classified as sources. For these nine studies, anthropogenic causes of source-sink dynamics were more commonly investigated and more commonly found to occur than causes associated with natural habitat quality.

Studies listed above notwithstanding, the confusion surrounding the definition of sinks makes assessing the commonality and causes of source-sink dynamics difficult. This situation underlines a need to develop a common definition for sources and sinks that can be incorporated in both theoretical and empirical research and that will be useful

25

in scientific, management, and conservation efforts. If sources are to be viewed as local populations that are valuable to the system of interest, whereas sinks are detrimental (e.g., Semlitsch 2000), then C^r may be the best single criterion for evaluating local populations.

Bridging the Gap between R^r and C^r in Empirical Studies

One key question when we are unable to estimate emigration rates is: Would the additional consideration of emigration rates change our classification of populations from sink to source? Perhaps the best way of answering this is to numerically solve C^r for the two unknowns (ϕ_A^{12}, ϕ_J^{12}), given R^r, and analyze how the unknowns may affect source-sink classification. As an example, assume a two-population system in which $\phi_A^{11} = 0.55$ and $\phi_J^{11} = 0.3$ for females in a population of *Seiurus aurocapillus* (ovenbirds) and in which each female produces 0.6 female young per year (estimates roughly corresponding to those used by Donovan et al. [1995]). Using equation (5) to calculate R^r, we classify the habitat as a sink because $0.55 + 0.3(0.6) < 1$. However, if we wish to incorporate emigration in our classification then we see, after algebraic rearrangement of equation (6), that the population is actually a source if $\phi_A^{12} + 0.6(\phi_J^{12}) > 0.27$. In figure 3, we present a range of values for (ϕ_A^{12}, ϕ_J^{12}) that would change the classification of the population from sink to source. For instance, if adults had a combined survival/emigration probability of 0.15, and juveniles had a combined survival/emigration probability of 0.25 (e.g., Hobson et al. 2004), the habitat in question would be a source rather than a sink (point A). If, however, the adult and juvenile survival/emigration probabilities were 0.05 and 0.15, the habitat would be a sink (point B). Reporting such patterns may be useful in empirical studies that cannot estimate

26

emigration because it allows informed readers to assess the likelihood of source-sink dynamics occurring given possible rates of emigration.

Discussion

Describing the Role of Local Sites

The "contribution" metric (C^r, eq. [4]) describes the proportional contribution a local population makes in one time-step to the metapopulation: for each individual in the local population at time t, there will be C^r individuals in the entire metapopulation at time $t+1$. We believe that this metric is an appropriate and valuable descriptor of the role a local population plays in the metapopulation for the following reasons: First, C^r remains true to the spirit of Pulliam's λ. If $C^r < 1$, the local population can be considered a sink because it represents a net loss to the metapopulation. Second, C^r incorporates the process of emigration and is thus able to distinguish cases that differ in the rate of mortality during emigration. Third, the equation for C^r (4) clearly shows which parameter estimates are useful for quantifying contributions of local populations. Therefore, use of C^r should avoid past errors of misinterpretation associated with other criteria (e.g., use of apparent survival in place of true survival). Fourth, C^r has a clear connection to the asymptotic growth rate of the metapopulation. Finally, measurement of C^r occurs over one-time step and correspondingly requires no asymptotic assumptions.

Thus, we believe C^r is an appropriate metric for describing the role a local population plays in its metapopulation because it integrates the processes of local recruitment, survival, site fidelity, and emigration but assumes nothing about population equilibrium. Other metrics, when used singly to evaluate local populations, involve

27

assumptions about dispersal and population equilibrium that may not apply in many situations.

Although the contribution metric offers an apt description of the role a local population plays, simultaneous consideration of multiple metrics (C^r, R^r, λ^r_{loc}, E^r and I^r) allows for a much richer description. For instance, if $C^r > 1$ but $R^r < 1$, then the local population is a "dependent source", i.e., a net contributor to the landscape that nevertheless requires gains from immigration to offset losses from emigration. The additional consideration of λ^r_{loc} allows for description of populations that are not at equilibrium, a valuable addition because non-equilibrium conditions brought on by both natural and anthropogenic disturbance are widely recognized to be a common ecological situation (Pickett and White 1985, Fahrig and Merriam 1994, Tilman 1999) with potentially profound implications for conservation of declining species (e.g., Jones et al. 2001).

Spatial, Temporal, and Statistical Considerations

Emigration from sampled areas. Even when multiple populations are sampled, individuals may emigrate from the sample space (Franklin et al. 2004). If the system of interest is larger than the sampled area, then out-of-sample-space emigration leads to a negative bias in survival estimates and a corresponding tendency to classify sources as sinks. Thus, the definition of sinks may be scale-dependent in that a location defined as a sink with respect to a narrowly defined study system may be defined as a source when considered with respect to a larger system. This underlines the importance of delineating the system of interest according to biological, rather than sampling, concerns. Many studies may not be able to sample all local populations within the system of interest. In

28

some study systems, all local populations may exhibit $C^r < 1$. This situation may be relatively common in taxa such as small mammals and songbirds. If so, accurate identification of sources and sinks may be very difficult, and consideration of the relative value of the C^r's, rather than a dichotomous source/sink classification, may be most useful for evaluating the value of local populations.

Temporal variation. Because vital rates can exhibit temporal variation, so can local populations, and areas that are sources one year may be sinks the next. For instance, Stacey and Taper (1992) found considerable annual variation in reproductive and apparent survival rates for *Melanerpes formicivorus* (acorn woodpecker). Another example involves density-dependent reproduction: if reproduction varies inversely with density in source populations, sources may appear to be sinks (Watkinson and Sutherland 1995). This tendency is problematic for empirical studies of source-sink dynamics because density-dependent reproduction is difficult to identify in unmanipulated populations. These examples point to the importance of considering temporal variation in population parameters when investigating how local populations affect systems of interest (Thomas et al. 1996).

Estimates of Error. Uncertainty in parameter estimates leads to uncertainty in source-sink classification, and confidence intervals for metrics such as C^r would be helpful when investigating potential source-sink dynamics (Doncaster et al. 1997, Powell et al. 2000). For example, Ferrer and Donazar (1996) calculated a metric similar to C^r in a purported sink population as 0.97. A 95% confidence interval of C^r would likely contain numbers greater than one, thus rendering uncertain conclusions regarding source-sink classification.

29

Implications

The importance of a local population to the metapopulation has become an increasingly active area of research over the past decade, with substantial relevance to evolutionary and population ecology and crucial importance to conservation of wildlife habitat. Unfortunately, much of the research designed to explore proximate and ultimate causes of population structure across multiple sites has not adequately considered the role of emigration.

Emigration is a vitally important process for multisite populations. Any local population that exports individuals is valuable because it can reduce both extinction probability and genetic drift in the metapopulation. When we ignore emigration, we may underestimate the value of local populations. This, in turn, may lead to habitat management that does not accurately reflect the population dynamics of the species of concern. If our primary concern in investigating local populations is habitat management (as in many investigations of source-sink dynamics), then we need to quantify the rate or number of individuals that the habitat of interest is producing and then exporting. Without this estimate, habitat management for species with high dispersal rates (e.g., songbirds, waterfowl, small mammals) may be ineffective and potentially detrimental. By classifying local populations with the set of metrics presented in this manuscript, we should be able to advance understanding regarding proximate and ultimate causes of population structure across the landscape.

30

Acknowledgments.

Appendix A Chapter 2. Alternate Estimation of Contribution

C^r for Structured Populations

Extending the definition of the "contribution metric" to encompass structured local

populations is straightforward and accomplished in two steps. First, consider each age-

(or stage-) class within a site to be its own "site" and construct its own contribution

metric as the column sum of the metapopulation transition matrix. Second, weight the

contribution metrics for the ages within a site by their current (relative) abundances.

For example, consider a population with two local sites and structured dynamics

that require three age-classes. The transition matrix is given by

$$\mathbf{A} = \begin{bmatrix} \beta_1^1 \phi_J^{11} & \beta_2^1 \phi_J^{11} & \beta_A^1 \phi_J^{11} & \beta_2^2 \phi_J^{21} & \beta_2^2 \phi_J^{21} & \beta_A^1 \phi_J^{21} \\ \phi_1^{11} & 0 & 0 & \phi_1^{21} & 0 & 0 \\ 0 & \phi_2^{11} & \phi_A^{11} & 0 & \phi_2^{21} & \phi_A^{21} \\ \beta_1^1 \phi_J^{12} & \beta_2^1 \phi_J^{12} & \beta_A^1 \phi_J^{12} & \beta_1^2 \phi_J^{22} & \beta_2^2 \phi_J^{22} & \beta_A^2 \phi_J^{22} \\ \phi_1^{12} & 0 & 0 & \phi_1^{22} & 0 & 0 \\ 0 & \phi_2^{12} & \phi_A^{12} & 0 & \phi_2^{22} & \phi_A^{22} \end{bmatrix} \tag{A1}$$

where the superscripts refer to sites (and transitions among sites) and the subscripts refer

to ages. The contribution of, say, age class 2 at site 1 to the entire metapopulation in the

next time step is given by

$$C_2^1 = \phi_2^{11} + \phi_2^{12} + \beta_2^1 \phi_J^{11} + \beta_2^1 \phi_J^{12}, \tag{A2}$$

which is the sum of the second column of $\mathbf{A}$. The contribution of each age-class within

each site is given by the column sum of the transition matrix

$$\mathbf{C}' = \begin{bmatrix} C_1^1 & C_2^1 & C_A^1 & C_1^2 & C_2^2 & C_A^2 \end{bmatrix} = \mathbf{1}'\mathbf{A} . \tag{A3}$$

32

Importantly, this definition for the contributions holds more generally for all forms of transitions within the sites, that is, it holds for stage-transition matrices as well as age-transition matrices whether the matrix contains spatial structure or not.

To combine the contributions for the age-classes into a single contribution for a particular site, the age-specific contributions should be weighted by the relative abundances. For example, the contribution of site 1 (in the system represented by $\mathbf{A}$ above) is

$$C_\bullet^1 = \frac{\sum_{k=1}^{a} C_k^1 N_k^1}{\sum_{k=1}^{a} N_k^1} . \tag{A4}$$

Weighting by the current abundances (or relative abundances), rather than the stable age-distribution, has the advantage of avoiding asymptotic assumptions while expressing the current contribution of the site. However, there may be applications where weighting by the stable age-distribution produces a more appropriate inference. For instance, if a longer-term view is to be taken, then the contribution of a site is given by

$$C_\bullet^1 = \sum_{k=1}^{a} C_k^1 w_k^1 , \tag{A5}$$

where $\mathbf{w}^1$ is the stable age distribution from $\mathbf{A}$, for the age-classes in site 1, normalized so that $\mathbf{1'w}^1 = 1$.

Estimating Seniority for Local Populations

Assume a system of 2 local populations that is geographically closed (no movement to or from other local populations). Define the seniority parameter $\gamma_t^{rs(l)}$ as the probability that an adult present in local population r at time t was an animal of age l (0=juvenile, 1=adult) in local population s at time $t-1$.

33

The growth rate of the entire system can be written as

$$\frac{N_{t+1}^1 + N_{t+1}^2}{N_t^1 + N_t^2},$$ (A6)

where N_t^r is the number of adults in local population r at time t. The contribution of local population 1 to the growth of the system involves both individuals that remained in local population 1 between t and $t+1$, $N_{t+1}^1(\gamma_{t+1}^{11(1)} + \gamma_{t+1}^{11(0)})$, and individuals that moved from local population 1 to local population 2 between t and $t+1$, $N_{t+1}^2(\gamma_{t+1}^{21(1)} + \gamma_{t+1}^{21(0)})$. The proportional contribution of local population 1 to the numerator of equation (A1), and hence to the growth of the system, can thus be written as

$$\frac{N_{t+1}^1(\gamma_{t+1}^{11(1)} + \gamma_{t+1}^{11(0)}) + N_{t+1}^2(\gamma_{t+1}^{21(1)} + \gamma_{t+1}^{21(0)})}{N_{t+1}^1 + N_{t+1}^2}.$$ (A7)

The numerator of (12) simply expresses the number of animals in the population at time $t+1$ that were either surviving adults from local population 1 at time t or new recruits produced in local population 1 at t. A similar expression can be written for the contribution of local population 2.

34

Appendix B Chapter 2. Review of Empirical Studies

138 papers published from 1981-2001 that used empirical estimates to classify local populations of vertebrates as sources and sinks. For parameters used to assess source sink status, N is abundance, B indicates some estimate of birth rate (nest success, number of juveniles, etc.), ϕ is combined probability of survival and philopatry, S is probability of survival, λ is local population growth rate, P/A is presence-absence, E and I indicate both per capita and count estimates of emigration and immigration, Gen indicates genetic data were used, and (sim) indicates that data were simulated or obtained from a literature source that estimated vital rates in a geographically separate population. Subscript A refers to breeding age individuals, subscript J to pre-breeding age individuals. The "Crit." column denotes the type of criterion used to classify local populations with criteria explained in text. The "focal populations" field was evaluated only for research that estimated appropriate criteria from data obtained in local populations of interest.

Author(s)	Year	Article Title	Journal	Parameters	Crit.	Focal populations
Adler et al.	1984	Characteristics of white-footed mice *Peromyscus leucopus* in woodland and grassland in eastern Massachusetts, USA	Acta Theriologica 29:57-62	N		
Anders et al.	1997	Juvenile survival in a population of neotropical migrant birds	Conservation Biology 11:698-707	B, ϕ_J, ϕ_A (sim)		
Andersen	1994	Demographics of small mammals using anthropogenic desert riparian habitat in Arizona	Journal of Wildlife Management 58:445-454	N, B, ϕ_J, ϕ_A	R'	Sources and sink
Barbour & Litvaitis	1993	Niche dimensions of New England cottontails in relation to habitat patch size	Oecologia 95:321-327	N, S_A		
Begazo & Bodmer	1998	Use and conservation of Cracidae (Aves: Galliformes) in the Peruvian Amazon	Oryx 32:301-309	N, B		
Beshkarev et al.	1994	Long-term dynamics of hazel grouse populations in source- and sink-dominated pristine taiga landscapes	Oikos 71:375-380	N		
Blondel et al.	1992	Do harlequin Mediterranean environments function as source-sink for blue tits *Pareus caeruleus* L.?	Landscape Ecology 6:213-219	B		

35

Author	Year	Title	Citation	Parameters	R²	Sources and sinks
Blondel et al.	1993	Habitat heterogeneity and life-history variation of Mediterranean blue tits (*Parus caeruleus*)	Auk 110:511-520	B		
Blondel et al.	2001	Is phenotypic variation of blue tits (*Parus caeruleus* L.) in Mediterranean mainland and insular landscapes adaptive?	Genetics-Selection-Evolution 33:S121-S139	B, Gen		
Bollinger et al.	1997	Status of Neotropical migrants in three forest fragments in Illinois	Wilson Bulletin 109:521-526	B		
Brandle & Moseby	1999	Comparative ecology of two populations of *Pseudomys australis* in northern South Australia	Wildlife Research 26:541-564	N, B		
Brandle et al.	1999	The distribution, habitat requirements and conservation status of the plains rat, *Pseudomys australis* (Rodentia: Muridae)	Wildlife Research 26:463-477	P/A		
Brawn & Robinson	1996	Source-sink population dynamics may complicate the interpretation of long-term census data	Ecology 77:3-12	λ'_{loc}, B		
Breininger et al.	1995	Landscape patterns of Florida Scrub Jay habitat use and demographic success	Conservation Biology 9:1442-1453	N, B, ϕ_j, ϕ_A, I, E		
Brook & Kikkawa	1998	Examining threats faced by island birds: A population viability analysis on the Capricorn silvereye using long-term data	Journal of Applied Ecology 35:491-503	λ'_{loc}, B, ϕ_j, ϕ_A, I (sim), E (sim)		
Bryant	1996	Reproduction and persistence of Vancouver Island marmots (*Marmota vancouverensis*) in natural and logged habitats	Canadian Journal of Zoology 74:678-687	B, ϕ_j, ϕ_A,		
Budnik et al.	2000	Demography of Bell's Vireos in Missouri grassland-shrub habitats	Auk 117:925-935	N, B, ϕ_j (sim), ϕ_A		
Burke & Nol	2000	Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario	Ecological Applications 10:1749-1761	B, ϕ_j (sim), ϕ_A (sim)		
Celada et al.	1994	Occupancy of isolated woodlots by the red squirrel *Sciurus vulgaris* L. in Italy	Biological Conservation 69:177-183	P/A		

36

Author	Year	Title	Citation			Notes
Clergeau & Burel	1997	The role of spatio-temporal patch connectivity at the landscape level: An example in a bird distribution	Landscape and Urban Planning 38:37-43	P/A		
Clinchy et al.	2001	Dispersal sinks and handling effects: Interpreting the role of immigration in common brushtail possum populations	Journal of Animal Ecology 70:515-526	B, S_i, S_A, I	C	Sinks caused by handling effects
Cunningham et al.	2001	Age structure, survival, and mortality of mountain lions in Southeastern Arizona	Southwestern Naturalist 46:76-80	S_A		
Curnutt et al.	1996	Population variability of sparrows in space and time	Oikos 76:131-144	N		
De Bruijn	1994	Population ecology and conservation of the Barn Owl *Tyto alba* in farmland habitats in Liemers and Achterhoek (The Netherlands)	Ardea 82:1-109	$\lambda^r_{loc}, B, \phi_j, \phi_A, I, E$	R	Sources and sinks
Delattre et al.	1999	Vole outbreaks in a landscape context: Evidence from a six year study of *Microtus arvalis*	Landscape Ecology 14:401-412	N		
Dias et al.	1994	Blue tits in Mediterranean habitat mosaics	Ardea 82:363-372	B		
Dias et al.	1996	Source-sink populations in Mediterranean blue tits: Evidence using single-locus minisatellite probes	Journal of Evolutionary Biology 9:965-978	Gen		
Dias & Blondel	1996	Local specialization and maladaptation in the Mediterranean blue tit (*Parus caeruleus*)	Oecologia 107:79-86	B		
Diffendorfer	1998	Testing models of source-sink dynamics and balanced dispersal	Oikos 81:417-433	$\lambda^r_{loc}, B, \phi_j = \phi_A, I, E$		
Diffendorfer et al.	1995	Habitat fragmentation and movements of three small mammals (Sigmodon, microtus, and Peromyscus)	Ecology 76:827-839	N, I, E		
Dmowski et al.	1995	Ecological effects of heavy metal pollution (Pb, Cd, Zn) on small mammal populations and communities	Bull. Pol. Acad. Sci. Biol. Sci. 43:1-10	N, B		

37

Author	Year	Title	Citation	Variables		Category
Donald & Evans	1995	Habitat selection and population size of Corn Buntings *Miliaria calandra* breeding in Britain in 1993	Bird Study 42:190-204	N		Sources and sinks
Doncaster et al.	1997	Balanced dispersal between spatially varying local populations: An alternative to the source-sink model	American Naturalist 150:425-445	λ_{loc}, B, ϕ_I, ϕ_A, I, E	C?	
Donovan et al.	1995	Reproductive success of migratory birds in habitat sources and sinks	Conservation Biology 9:1380-1395	N, B, ϕ_I (sim), ϕ_A		
Doyle, A.T.	1990	Use of riparian and upland habitats by small mammals	Journal of Mammalogy 71:14-23	N		
Duguay et al.	2001	Songbird abundance and avian nest survival rates in forests fragmented by different silvicultural treatments	Conservation Biology 15:1405-1415	N, B		
Duhamel et al.	2000	Landscape effects on the population dynamics of the fossorial form of the water vole (*Arvicola terrestris sherman*)	Landscape Ecology 15:89-98	P, A		
Ellison & Van Riper	1998	A comparison of small-mammal communities in a desert riparian floodplain	Journal of Mammalogy 79:972-985	N		
Eriksson et al.	2001	Nest-predation at the edge: An experimental study: contrasting two types of edges in the dry Chaco, Paraguay	Ecography 24:742-750	B		
Etheridge et al.	1997	The effects of illegal killing and destruction of nests by humans on the population dynamics of hen harriers *Circus cyaneus* in Scotland	Journal of Applied Ecology 34:1081-1105	B, S_J, ϕ_A, I, E	C?	Sources and sink
Fauth	2000	Reproductive success of Wood Thrushes in forest fragments in northern Indiana	Auk 117:194-204	B, ϕ_I (sim), ϕ_A		
Fauth	2001	Wood Thrush populations are not all sinks in the agricultural midwestern United States	Conservation Biology 15:523-527	B, ϕ_I (sim), ϕ_A		
Fauth et al.	2000	Using landscape metrics to model source habitat for Neotropical migrants in the midwestern U.S.	Landscape Ecology 15:621-631	N, B		

38

Author	Year	Title	Citation	Parameters		Source/sink
Ferrer & Donazar	1996	Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles	Ecology 77:69-74	N, B, S_J, S_A	C	Source and sink
Flaspohler et al.	2001	Species-specific edge effects on nest success and breeding bird density in a forested landscape	Ecological Applications 11:32-46	N, B		
Flaspohler et al.	2001	Effects of forest edges on Ovenbird demography in a managed forest landscape	Conservation Biology 15:173-183	N, B, ϕ_J (sim), ϕ_A		
Foppen et al.	2000	Understanding the role of sink patches in source-sink metapopulations: Reed Warbler in an agricultural landscape	Conservation Biology 14:1881-1892	N		
Ford et al.	2001	Reproductive success of forest-dependent songbirds near an agricultural corridor in south-central Indiana	Auk 118:864-873	B, ϕ_J (sim), ϕ_A		
Friesen et al.	1999	Nesting success of Neotropical migrant songbirds in a highly fragmented landscape	Conservation Biology 13:338-346	B, ϕ_J (sim), ϕ_A		
Fryxell	2001	Habitat suitability and source-sink dynamics of beavers	Journal of Animal Ecology 70:310-316	N, B		
Gagen et al.	1998	Ouachita madtom (*Noturus lachneri*) metapopulation dynamics in intermittent Ouachita Mountain streams	Copeia 1998:874-882	$\lambda_{loc}, I=0, E=0$	C	Sources and sinks
Gaona et al.	1998	Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*)	Ecological Monographs 68:349-370	$\lambda_{loc}, B, S_J, S_A, I, E$	C	Sources and sinks
Geertsma et al.	2000	Are high fitness values sufficient to maintain a Dutch population of the red-backed shrike (*Lanius collurio*)?	The Ring 22:79-88	N, B, ϕ_J, ϕ_A	R	Sink
Graves	1997	Geographic clines of age ratios of black-throated blue warblers (*Dendroica caerulescens*)	Ecology 78:2524-2531	N, B		
Hanley & Barnard	1999	Spatial variation in population dynamics of Sitka mice in floodplain forests	Journal of Mammalogy 80:866-879	N, ϕ_J, ϕ_A, I, E		

39

Author	Year	Title	Source			
Hansen et al.	1999	Dynamic habitat and population analysis: An approach to resolve the biodiversity manager's dilemma	Ecological Applications 9:1459-1476.	N, B, ϕ_1 (sim), ϕ_A		
Hatchwell et al.	1996	The demography of blackbirds *Turdus merula* in rural habitats: Is farmland a sub-optimal habitat?	Journal of Applied Ecology 33:1114-1124	B, ϕ_1, ϕ_A, I, E	$R^?$	Sinks only
Hejl et al.	1988	Weather and bird populations in true fir forests of the Sierra Nevada California USA	Condor 90:561-574	N		
Holmes et al.	1996	Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics	Journal of Animal Ecology 65:183-195	N, B, ϕ_A		
Hoover et al.	1995	Effects of forest patch size on nesting success of wood thrushes	Auk 112:146-155	B		
Horskins et al.	1998	Habitat usage of *Rattus rattus* in Australian macadamia orchard systems: Implications for management	Crop Protection 17:359-364	N, I, E		
Hunt	1998	Evidence from a metapopulation model of the importance of early successional habitat to the American Redstart	Conservation Biology 12:1377-1389	$\lambda^r_{loc}, B, \phi_1$ (sim), ϕ_A (sim)	λ^r_{loc}	
Jarvinen & Vaisnan	1984	Reproduction of pied flycatchers *Ficedula hypoleuca* in good and bad breeding seasons in a northern marginal area	Auk 101:439-450	B		
Johannesen et al.	2000	Spatial explicit demography: The effects habitat patch isolation have on vole matrilines	Ecology Letters 3:48-57	$\lambda^r_{loc}, B, \phi_1, \phi_A, I, E$		
Keith et al.	1993	Dynamics of a snowshoe hare population in fragmented habitat	Canadian Journal of Zoology 71:1385-1392	N, B, S_1, S_A, I, E		
Kershner & Bollinger	1996	Reproductive success of grassland birds at East-central Illinois airports	American Midland Naturalist 136:358-366	N, B		
Kim et al.	1998	Habitat islands, genetic diversity, and gene flow in a Patagonian rodent	Molecular Ecology 7:667-678	Gen		

40

Author	Year	Title	Source			
Knight et al.	1988	Mortality patterns and population sinks for Yellowstone grizzly bears, 1973-1985	Wildlife Society Bulletin 16:121-125	S_A		
Kontio et al.	1998	Resilience of a Minnesota black bear population to heavy hunting: Self-sustaining population or population sink?	Ursus 10:139-146	N, B, S_A, I		
Kozakiewicz et al.	1999	Effects of habitat fragmentation on four rodent species in a Polish farm landscape	Landscape Ecology 14:391-400	N		
Krohne	1989	Demographic characteristics of Peromyscus leucopus inhabiting a natural dispersal sink	Canadian Journal of Zoology 67:2321-2325	N		
Krohne & Baccus	1985	Genetic and ecological structure of a population of Peromyscus leucopus	Journal of Mammalogy 66:529-537	N, I, E		
Labbe & Fausch	2000	Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales	Ecological Applications 10:1774-1791	B, ϕ_i, ϕ_A, I, E		
Lariviere et al.	2000	Status and conservation of the gray wolf (Canis lupus) in wildlife reserves of Quebec	Biological Conservation 94:143-151	N		
Limo & Jaksic	1999	Survival, recruitment, and immigration processes in four subpopulations of the leaf-eared mouse in semiarid Chile	Oikos 85:343-355	N, B, ϕ_i, ϕ_A, I		
Lin & Batzli	2001	The influence of habitat quality on dispersal, demography, and population dynamics of voles	Ecological Monographs 71:245-275	$\lambda_{loc}, B, S_i, S_A, I, E$	C	Sources only
Linzey	1989	Response of the white-footed mouse Peromyscus leucopus to the transition between disturbed and undisturbed habitats	Canadian Journal of Zoology 67:505-512	N		
Luttrell et al.	1999	Declining status of two species of the Macrhybopsis aestivalis complex (Teleostei: Cyprinidae) in the Arkansas River Basin and related effects of reservoirs as barriers to dispersal	Copeia 1999:981-989	P, A		

41

Author	Year	Title	Journal	$\lambda_{loc}, B, S_j, S_A, I, E$	C'	Source and sinks
Mace & Waller	1998	Demography and population trend on grizzly bears in the Swan Mountains, Montana	Conservation Biology 12:1005-1016			
Martell	1983	Demography of southern red-backed voles *Clethrionomys gapperi* and deer mice *Peromyscus maniculatus* after logging in north central Ontario, Canada	Canadian Journal of Zoology 61:958-969	N, B, ϕ_j, ϕ_A		
Martell	1984	Changes in small mammal communities after fire in northcentral Ontario, Canada	Canadian Field Naturalist 98:223-226	N		
Martin & Szuter	1999	War zones and game sinks in Lewis and Clark's west	Conservation Biology 13:36-45	N		
Matthews	1990	A comparative study of habitat use by young-of-the-year subadult and adult rockfishes on four habitat types in central Puget Sound Washington, USA	Fishery Bulletin 88:223-240	N		
McCoy et al.	1999	Conservation Reserve Program: Source or sink habitat for grassland birds in Missouri?	Journal of Wildlife Management 63:530-538.	N, B, ϕ_j (sim), ϕ_A		
McCoy et al.	2001	Grassland bird conservation: CP1 vs. CP2 plantings in conservation reserve program fields in Missouri	American Midland Naturalist 145:1-17	N, B		
McGowan & Otis	1998	Population demographics of two local South Carolina mourning dove populations	Journal of Wildlife Management 62:1443-1451	B, S_j, S_A	C'	Sink
Meserve et al.	1999	The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: Results of a long-term experiment	Oikos 85:364-372	N		
Mladenoff et al.	1995	A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region	Conservation Biology 9:279-294	N, E		
Mladenoff et al.	1999	Predicting gray wolf landscape recolonization: Logistic regression models vs. new field data	Ecological Applications 9:37-44	P/A		

42

Author	Year	Title	Source	B, ϕ_i, ϕ_A, I, E	R	Source and sink
Mumme et al.	2000	Life and death in the fast lane: Demographic consequences of road mortality in the Florida Scrub-Jay	Conservation Biology 14:501-512	B, ϕ_i, ϕ_A, I, E		
Murphy	2001	Habitat-specific demography of a long-distance, neotropical migrant bird, the Eastern Kingbird	Ecology 82:1304-1318	λ^r_{loc}, B, ϕ_i (sim), ϕ_A, I, E		
Naylor et al.	1985	High density of heather voles *Phenacomys intermedius* in jack pine *Pinus banksiana* forests in Ontario, Canada.	Canadian Field Naturalist 99:494-497	N		
Ostfeld & Klosterman	1986	Demographic substructure in a California vole *Microtus californicus* population inhabiting a patchy environment	Journal of Mammalogy 67:693-704	N, B, ϕ_i, ϕ_A, I, E		
Ouin et al.	2000	Spatial dynamics of wood mouse (*Apodemus sylvaticus*) in an agricultural landscape under intensive use in the Mont Saint Michel Bay (France)	Agric. Ecosys. Environ. 78:159-165	N		
Paradis	1995	Survival, immigration and habitat quality in the Mediterranean pine vole	Journal of Animal Ecology 64:579-591	N, B, ϕ_i, ϕ_A, I		
Paradis et al.	1993	Estimation of sex- and age-related survival rates in a microtine population	Journal of Wildlife Management 57:158-163	ϕ_i, ϕ_A,		
Peres	2001	Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates	Conservation Biology 15:1490-1505	N		
Porneluzi & Faaborg	1999	Season-long fecundity, survival, and viability of ovenbirds in fragmented and unfragmented landscapes	Conservation Biology 13:1151-1161	N, B, ϕ_i (sim), ϕ_A,		
Porneluzi et al.	1993	Reproductive performance of territorial ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania	Conservation Biology 7:618-622	N, B		
Purcell & Verner	1998	Density and reproductive success of California towhees	Conservation Biology 12:442-450	N, B, ϕ_i (sim), ϕ_A (sim)		

43

				P/A	*R²*	
Rahbek	1997	The relationship among area, elevation, and regional species richness in neotropical birds	American Naturalist 149:875-902	*P/A*		
Rejinen & Foppen	1994	The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for willow warblers (*Phylloscopus trochilus*) breeding close to a highway	Journal of Applied Ecology 31:85-94.	$N, B, \phi_l, \phi_A, I, E$		
Foppen & Rejnen		The effects of car traffic on breeding bird populations in woodland. II. Breeding dispersal of male willow warblers (*Phylloscopus trochilus*) in relation to the proximity of a highway	Journal of Applied Ecology 31:95-101			
Rejinen & Foppen	1995	The effects of car traffic on breeding bird populations in woodland. IV. Influence of population size on the reduction of density close to a highway	Journal of Applied Ecology 32:481-491	N		
Robinson & Wilcove	1994	Forest fragmentation in the temperate zone and its effects on migratory songbirds	Bird Conservation International 4:233-249	N, B	.	
Robinson et al.	1995	Regional forest fragmentation and the nesting success of migratory birds	Science 267:1987-1990	B		
Rogers et al.	1997	Nest predation and cowbird parasitism create a demographic sink in wetland-breeding song sparrows	Condor 99:622-633	N, B, ϕ_l (sim), ϕ_A		
Rosenfield et al.	2000	Comparable reproductive success at conifer plantation and non-plantation nest sites for Cooper's Hawks in Wisconsin	Wilson Bulletin 112:417-421	B		
Roth & Johnson	1993	Long-term dynamics of a wood thrush population breeding in a forest fragment	Auk 110:37-48	N, B, ϕ_l (sim), ϕ_A, I		
Rowe et al.	2001	Failed recruitment of southern toads (*Bufo terrestris*) in a trace element-contaminated breeding habitat: Direct and indirect effects that may lead to a local population sink	Arch. Environ. Contam. Toxicol. 40:399-405	ϕ_l		Sinks only

44

Author	Year	Title	Citation		R'	Sources and sinks
Runstrom et al.	2001	Population statistics for paddlefish in the Wisconsin River	Trans. Am. Fish. Soc. 130:546-556.	N, ϕ_A,		
Saab & Vierling	2001	Reproductive success of Lewis's Woodpecker in burned pine and cottonwood riparian forests	Condor 103:491-501	B, ϕ_J (sim), ϕ_A (sim)		
Saether et al.	1999	Spatial and temporal variation in demography of a house sparrow metapopulation	Journal of Animal Ecology 68:628-637	N, B, ϕ_J, ϕ_A,		
Safford	1997	The destruction of source and sink habitats in the decline of the Mauritius Fody, *Foudia rubra*, an island-endemic bird	Biodiversity and Conservation 6:513-527	N, B		
Schlosser	1995	Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds	Ecology 76:908-925	N		
Schug et al.	1998	Isolation and genetic diversity of *Gambusia hubbsi* (mosquitofish) populations in blueholes on Andros Island, Bahamas	Heredity 80:336-346	Gen		
Simons et al.	2000	Evaluating Great Smoky Mountains National Park as a population source for the Wood Thrush	Conservation Biology 14:1133-1144	N, B, ϕ_J (sim), ϕ_A (sim)		
Sinsch	1997	Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation	Oecologia 112:42-47	B^*, ϕ_J, ϕ_A^*, I, E		
Skupski	1995	Population ecology of the western harvest mouse, *Reithrodontomys megalotis*: A long-term perspective	Journal of Mammalogy 76:358-367	N, B		
Stout & Demmer	1982	Cotton rat *Sigmodon hispidus* invasion of sand pine scrub habitat	Journal of Mammalogy 63:236-242	N		
Sullivan	1979	Demography of deer mice in coastal forest and clear-cut (logged) habitats	Canadian Journal of Zoology 57:1636-1648	N, B, ϕ_J, ϕ_A,		
Sullivan & Moses	1986	Red squirrel populations in natural and managed stands of lodgepole pine	Journal of Wildlife Management 50:595-601	N, B, ϕ_J, ϕ_A,		

45

Author	Year	Title	Journal	λ, B, ϕ_j, ϕ_A	R?	Sources and sinks
Tarkhnishvili et al.	1999	Spatial structure and regulation of a population of the brown frog *Rana macrocnemis* in Georgia	Herpetological Journal 9:167-177	λ, B, ϕ_j, ϕ_A,		
Tiebout & Anderson	2001	Mesocosm experiments on habitat choice by an endemic lizard: Implications for timber management	Journal of Herpetology 35:173-185	"Other"		
Torres et al.	1997	Spatiotemporal variability of rodent subpopulations at a semiarid neotropical locality	Journal of Mammalogy 78:505-513	N, B, I, E		
Toxopeus et al.	1993	Reproductive biology of the parsley frog, *Pelodytes punctatus*, at the northernmost part of its range	Amphibia-Reptilia 14:131-147	N, B		
Tremblay et al.	1998	Summer foraging behaviour of eastern coyotes in rural versus forest landscape: A possible mechanism of source-sink dynamics	Ecoscience 5:172-182	N, B		
Trenham et al.	2000	Life history and demographic variation in the California Tiger Salamander (*Ambystoma californiense*)	Copeia 2000:365-377	N, B, ϕ_A, I	R?	Sink
Trine	1998	Wood thrush population sinks and implications for the scale of regional conservation strategies	Conservation Biology 12:576-585	B, ϕ_j (sim), ϕ_A		
Van Horne	1981	Demography of *Peromyscus maniculatus* in seral stages of coastal conifer forests in southeast Alaska	Canadian Journal of Zoology 59:1045-1061	N, B, ϕ_j, ϕ_A,		
Vierling	2000	Source and sink habitats of Red-winged Blackbirds in a rural/suburban landscape	Ecological Applications 10:1211-1218	B, ϕ_j (sim), ϕ_A (sim)		
Virgl & Messier	2000	Assessment of source-sink theory for predicting demographic rates among habitats that exhibit temporal changes in quality	Canadian Journal of Zoology 78:1483-1493	λ^r_{loc}, B, ϕ_j (sim), ϕ_A, I, E	λ^r_{loc}	
Ward & Smith	2000	Brown-headed Cowbird parasitism results in a sink population in Warbling Vireos	Auk 117:337-344	λ^r_{loc}, B, ϕ_j (sim), ϕ_A (sim)		
Weinberg & Roth	1998	Forest area and habitat quality for nesting wood thrushes	Auk 115:879-889	B, ϕ_j (sim), ϕ_A, I		

46

					Sources and sinks
Wilson	1999	Bird feeding and irruptions in northern finches: Are migrations short-stopped?	North American Bird Bander 24:113-121	N, I, E	
Woodroffe & Ginsberg	1998	Edge effects and the extinction of populations inside protected areas	Science 280:2126-2128	N	
Wooten & Bell	1992	A metapopulation model of the peregrine falcon in California: Viability and management strategies	Ecological Applications 2:307-321	B, ϕ_j, ϕ_A, I (sim), E (sim)	
Yong et al.	1998	Stopover ecology and habitat use of migratory Wilson's warblers	Auk 115:829-842	"Other"	
Zanette	2000	Fragment size and the demography of an area-sensitive songbird	Journal of Animal Ecology 69:458-470	N, B, ϕ_j, ϕ_A	R

* Estimates of these processes from an earlier paper: Sinsch & Seidel 1995 Australian Journal of Ecology 20:351-36

47

Figure 1. Number of refereed papers published by year from 1979-2003 that explicitly investigated some aspect of source-sink dynamics (includes papers investigating dispersal sinks).
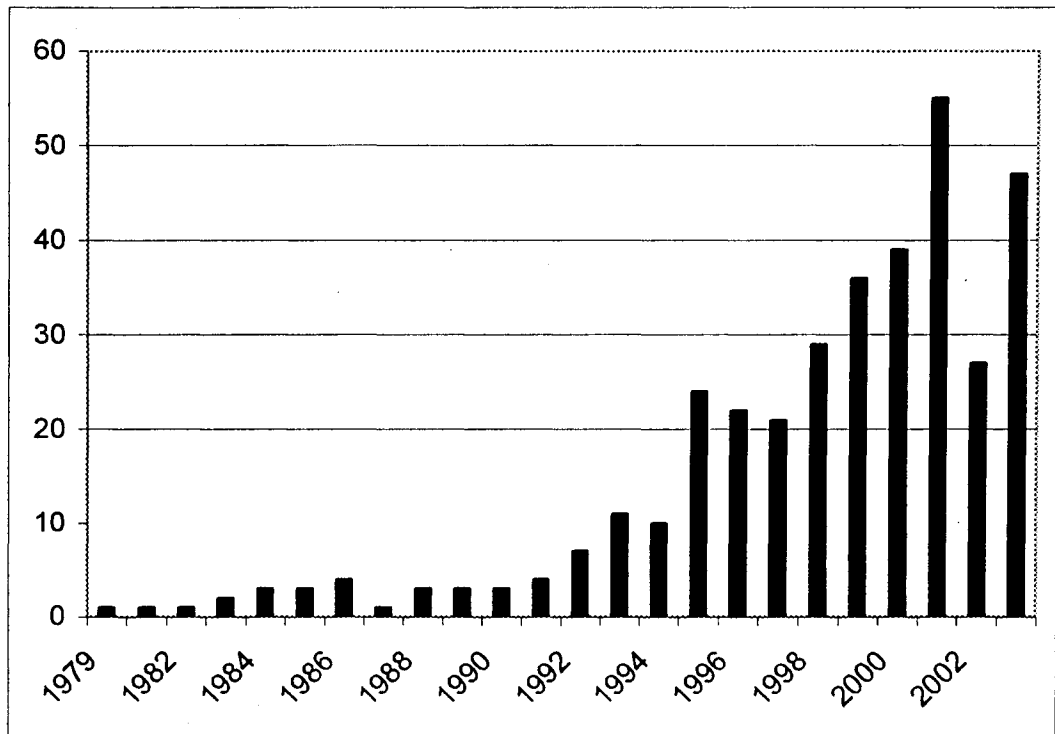
Figure 2. Number of refereed papers from 1979-2003 that attempted an empirical source-sink classification in a vertebrate population.
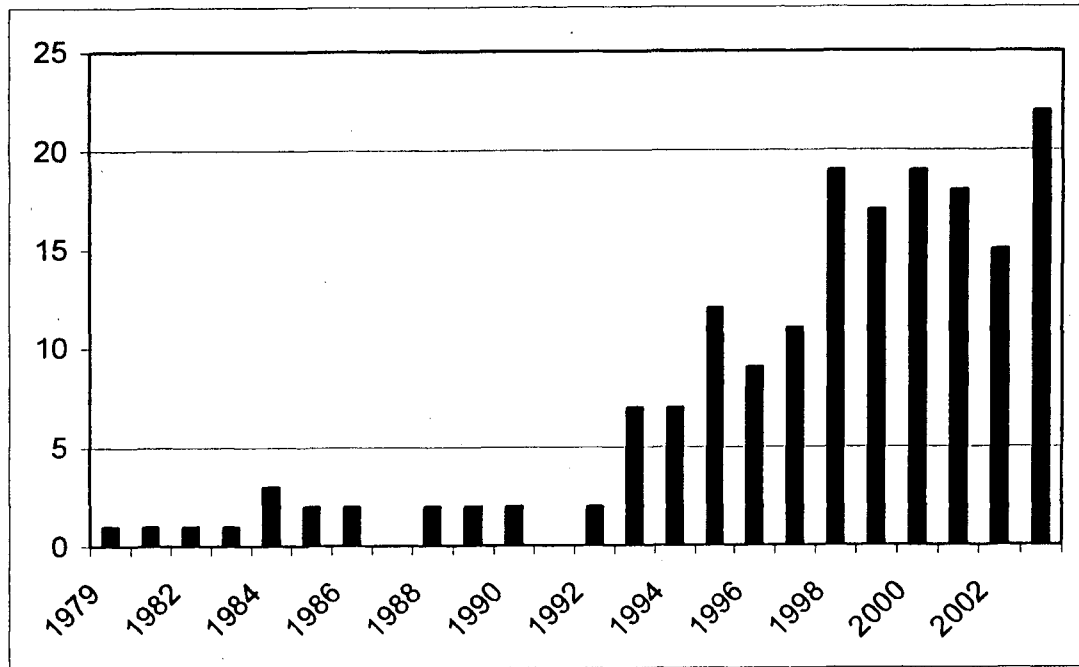
Figure 3. Classification of source-sink habitat for *Seiurus aurocapillus* using different values of ϕ_A^{12} and ϕ_J^{12} based on estimates of ϕ_A^{11}, ϕ_J^{11}, and β^1 from Donovan et al. (1995). Any point above the line would indicate habitat was a source, any point below a sink. At point A, ϕ_A^{12} is 0.25 and ϕ_J^{12} is 0.15, and the habitat is a source. At point B, ϕ_A^{12} is 0.05 and ϕ_J^{12} is 0.15, and the habitat is a sink.
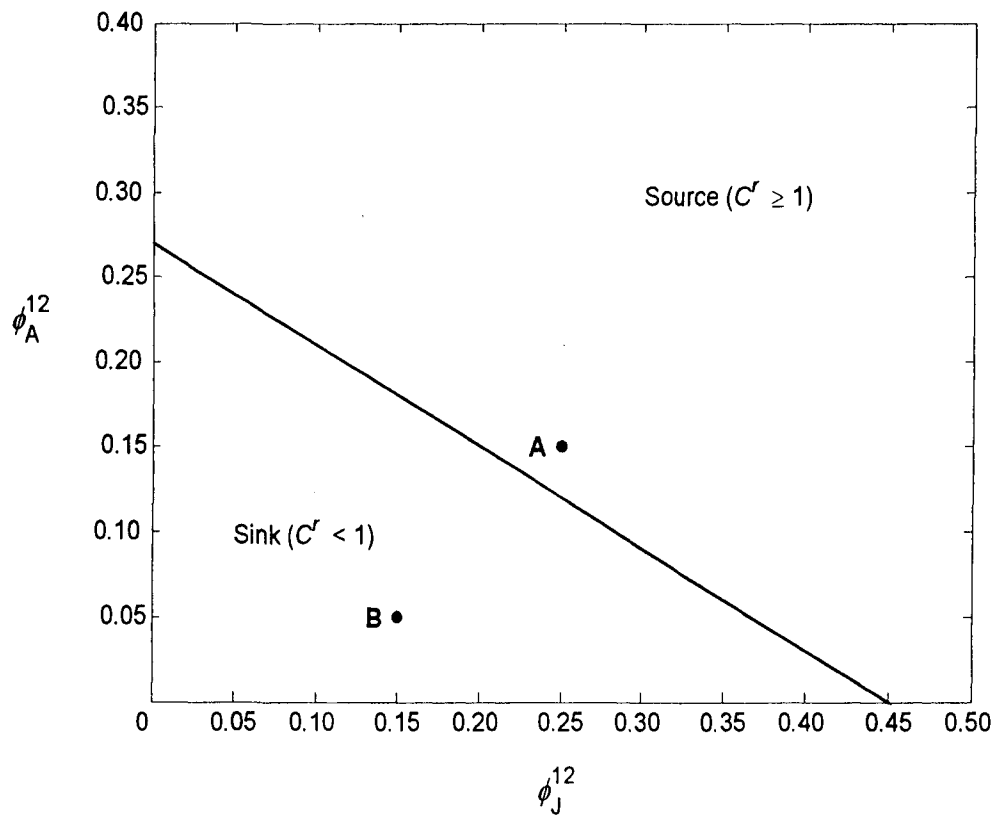
Chapter 3. Sources of variation in correct classification probability for two cryptic vole (*Microtus*) species

Abstract: *Microtus montanus* and *M. pennsylvanicus* are sister species with overlapping ranges throughout western North American. The two species compose an interesting system in which to study simultaneous effects of environmental variation, but accurately differentiating live specimens of the two species in field studies has been problematic. I used pelage color as the sole criterion to differentiate meadow and montane voles with an overall 92% rate of accuracy. Classification probability appeared to increase with observer experience and age of voles and varied by habitat. Differentiation of the two species via pelage coloration is possible for population-level studies. Future studies may improve upon methods presented here if pilot studies focusing solely on species identification are conducted.

Key words: species identification, *Microtus*, sister species, pelage coloration

Introduction

Correct assignment of individual organisms to species is crucial for many ecological studies, and variation in coloration patterns distinguishes most vertebrate species. Many mammals exhibit large variation in pelage color, however, limiting the usefulness of this criterion. Consequently, the use of pelage color to differentiate similar, co-occurring rodent species has met with varying degrees of success (Choate 1973, Burns et al. 1985, Bruseo et al. 1999).

Microtus pennsylvanicus (meadow vole) and *M. montanus* (montane vole) are sympatric throughout much of western North America and are difficult to differentiate

51

using characteristics measurable on live specimens. The two species compose an interesting study system for investigating patterns of habitat partitioning and competition (e.g., Koplin and Hoffmann 1968, Murie 1971, Hodgson 1972, Stroecker 1972, Colvin 1973, Douglass 1976a), but accurate identification of live specimens is important for the rigorous study of ecological relationships. Previously, pelage coloration and other external morphological features have proved unreliable for differentiating these two species (Hall 1981, Foresman 2001, Kays and Wilson 2002). Perhaps the only reliable method for differentiating live specimens is genetic sampling (Conroy and Cook 2000).

Pelage coloration in rodents may vary with age (Engstrom and Choate 1979, Lindquist et al. 2003), geographic location (Humphrey and Setzer 1989), and soil color (Heth et al. 1988, Krupa and Coluso 2000). Here I explore the probability of correctly identifying meadow and montane voles based on pelage color, including potential effects of age, sex, site, time, and habitat type. I present results of a three-year study in which approximately 92% of individuals were assigned correctly to species. This study shows how pelage color can accurately differentiate two sister species while detailing problems associated with the method and thus should be useful for future studies that must rely upon pelage color for species identification.

Materials and Methods

Procedures

The study was conducted in the Mission Valley of western Montana near the Ninepipes National Wildlife Refuge. Live trapping was conducted on five grids between June-August 2002 and four grids between May-September 2003 and 2004. Two grids of 160 medium-sized Sherman traps each were trapped simultaneously for 3-5 consecutive

nights. A livestock fence bisected each grid, thus one-half of each grid was grazed, and one-half was ungrazed. During 2002, traps were set in the evening and checked just before dawn. This schedule resulted in many trap mortalities. For cold nights in 2003 and 2004, traps were checked at least once during the night. In May of 2004 and September of 2003 and 2004, traps were set before dawn and checked in the afternoon, a schedule that reduced trap mortalities. Each vole handled was weighed, sexed, and received a provisional species classification. I alone was responsible for species classifications over the course of the study. Individuals that died in traps were identified to species based upon upper molar (M^2) pattern; meadow voles have a posterior loop in the M^2 that is absent in montane voles (Foresman 2001). Two hundred and ninety-three voles that died in traps received species classifications in the field and were subsequently analyzed for true species identification. Age was determined by weight, with montane voles < 15.0 g and meadow voles < 17.5g being classified as juveniles. These weight thresholds are lower than previously used (e.g., Keller and Krebs 1970) because many voles known to be $\geq$ 6 weeks old (thus technically subadults) were caught in multiple trapping sessions but never were observed to weigh greater than the thresholds listed above. Additionally, juvenile molts, which tended to be somewhat darker than adult molts, seemed to be present only in individuals less than 15.0g for montane voles and 17.5g for meadow voles. Handling protocol was approved by The University of Montana Institutional Animal Care and Use Committee and followed guidelines provided by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Predictor variables

53

Classification probability was expected to vary with the assignment of an individual to species based solely upon pelage color (hereafter, "species assignment"). In the Mission Valley, meadow voles tend to have reddish dorsal guard hairs and darker underfur, whereas montane voles have silver-tipped dorsal guard hairs and lighter underfur. However, meadow voles tend to exhibit more variation in pelage color than montane voles (Foresman 2001). Because meadow voles tend to resemble the "standard" coloration of montane voles more than vice versa, one would expect that a species assignment of montane vole would have a higher probability of being incorrect than a species assignment of meadow vole. Age may induce variation in classification probability because juveniles of both species tend to have darker molts than adults, making them more cryptic. Inter-individual coloration in voles may vary more in males because they have greater home ranges (Ostfeld 1986, Collins and Barrett 1997) and average dispersal distances (Sandell et al. 1990, Bollinger et al. 1993) and consequently have a greater likelihood of originating in habitat with different soil color or vegetation characteristics. Generally, one would expect classification probabilities to improve with observer experience, and therefore time. Time was analyzed both for year (2002-2004) and for week of the field season. Site was included as a variable because pelage color of rodents may vary over space (Humphrey and Setzer 1989, Krupa and Coluso 2000). Similarly, soil color in grazed areas tended to be lighter than in ungrazed areas. Thus voles surviving longer and reproducing in grazed areas may have lighter pelage color, which may result in differing classification probabilities by habitat. An additional variable considered was whether the species classification was made when the vole was

54

live or dead. Given that live voles are extremely active, they may be more difficult to identify to species.

Data Analysis

Logistic regression was conducted using S-Plus (Insightful Corp.) and data from 293 animals that died in traps and were identified to species based on dental patterns. Age, site, habitat, sex, species classification, state of the vole at the time of species classification (live or dead), year, and week within year were all included as predictor variables, and the binary response variable was whether the species classification was correct (1) or incorrect (0). Species classification, rather than true species, was used as a predictor variable because it is more consistent with parameterization of a capture-recapture model that can be used to estimate population parameters such as apparent survival, immigration, and emigration for situations in which species identity is not perfectly known (Runge et al. 2005b). For model selection, a very general model consisting of all *a priori* interaction terms was formulated. All interaction terms were then analyzed graphically before any statistical analysis, and any term in which the interaction was opposite to the *a priori* hypothesis was discarded. The resulting most general model considered is indicated in Table 1 and the full set of candidate models is presented in Appendix A. Models were ranked using Akaike's Information Criterion adjusted for small sample size (AICc) and the Bayesian Information Criterion (BIC). Model selection was conducted by stepwise progression starting from the most general model. If the deletion or addition of a parameter during the model selection process resulted in a lower BIC or AIC_c, then model selection continued. If BIC or AIC_c was higher for a more parsimonious model, then model selection stopped. Additionally,

55

multiple models with ≤ 10 parameters were examined to reduce the probability of converging to a local maximum for model likelihood. BIC has a higher penalty term for the number of parameters in the model and thus tends to select models with fewer explanatory variables. Generally, the model with the lowest AICc or BIC value is considered the best candidate model. Models within two AICc units of the model with the lowest AICc value are competitive candidates (Burnham and Anderson 2002). No analogous range exists for BIC. I used two AIC_c units and five BIC units as the cutoff value to include models in a best candidate subset. With a sample size of 293, any model with a score 5 BIC units above the best BIC model would include extra variables that explain very little variation in the data. Considerable controversy exists about which criterion is "best" to use in statistical analyses involving multiple predictor variables (e.g., Ripley 1996, Forster 2000, Burnham and Anderson 2002). One potential resolution is to test the stability of a model using cross-validation, which uses a large proportion of the data to generate a statistical model that is then used to predict values in a smaller, "held-out" fraction of the data (Stone 1974). I further evaluated the models in the best candidate subset using 10- and 5-fold cross-validation techniques, which hold out 10% and 20% of the data for predictive testing.

I used area under the receiver operating characteristic (ROC) curve as a measure of predictive accuracy to compare models. For each observation, model coefficients are multiplied by the predictor variables specific to that particular observation to assign a value between 0 and 1 to each individual. A critical value between 0 and 1 is then assigned, and if the model-based value is greater than the critical value, the response is labeled "positive"; if it is less, the response is labeled "negative". A positive, model-

56

based response for a set of predictor variables is considered correct if the response variable is 1 and incorrect if the response variable is 0 (the opposite is true for negative responses). The area under the ROC curve (hereafter, AUC) is then calculated by plotting measures of correct positive responses on the x-axis against incorrect negative responses on the y-axis for the range of critical values between 0 and 1. Thus AUC provides a measure of predictive accuracy for a given model by comparing the number of positive responses correctly predicted by the model with the number of negative responses incorrectly predicted. AUC values range between 0 and 1 with values less than 0.5 indicating discrimination worse than a coin flip, values between 0.5 and 0.6 suggesting discrimination little better than a coin flip, values between 0.6 and 0.7 suggesting fair discrimination, values between 0.7 and 0.8 suggesting acceptable discrimination, and values greater than 0.8 suggesting excellent discrimination (Hosmer and Lemeshow 2000). Each cross-validation process for each candidate model was repeated 20 times to generate a mean and standard deviation for the 20 estimated values of AUC. Assessing discriminatory ability with cross-validated data sets provides a measure of the ability of a statistical model to predict observations outside of a data set's scope and therefore may represent a valid approach if findings from a study are to guide future research. In this analysis I used AUC based upon 5-fold and 10-fold cross validation (hereafter, AUC5 and AUC10).

Results

The overall correct classification rate for voles, independent of any statistical modeling, was 91.5% (exact 95% binomial confidence interval [bin CI]: 87.7 – 94.4%). The correct classification rate was 94.1% for individuals positively identified as montane

57

voles (n = 135, 95% bin CI: 88.7 - 97.4%) and 89.2% for meadow voles (n = 158, 95% bin CI: 83.3 – 93.6%). Similarly, the correct classification rate was 88.2% for species assignments of montane vole (95% bin CI: 81.8-93.0%) and 94.6% for species assignments of meadow vole (95% bin CI: 89.7-97.7%) (Table 2).

Time, habitat, age, species assignment, and sex may have all influenced the probability of correct classification when controlling for multiple variables in a statistical model. In Table 1, a set of candidate models is ordered with AUC5, and results based upon AUC10, AICc, and BIC are also provided. The four statistical criteria all selected different models as the "best" model in the candidate set (Table 1). Thus, uncertainty exists regarding model selection and, correspondingly, sources of variation influencing classification probability. I present results from one of the more general models to elucidate variation in correct classification probability for the two vole species.

The model "species assignment*week + habitat + age + year + sex" was ranked first in terms of AUC5, second for AUC10, seventh for AICc, and extremely low for BIC (Table 1). The coefficient of 0.22 for the species assignment*week interaction term (Table 3) indicates that the probability for correct classification of individuals that received assignments of meadow vole may have improved each week of each field season relative to the correct classification for individuals that received assignments of montane vole (given constancy in the other variables in the model). Voles in grazed habitat had a significantly reduced probability of correct species classification (coefficient = -2.05). The age of voles appeared to induce some variation in classification probabilities; adult voles were correctly classified to species with greater probability than juveniles (coefficient = 1.15). Increasingly large coefficients in year two (0.80) and year

58

three (1.93) indicate that correct classification probability improved across field seasons. The positive coefficient for sex (0.55) indicates that females may have been easier to identify to species than males, although the confidence interval for sex was large and the term was absent from many of the best candidate models.

One test of the importance of a predictor variable in a logistic regression model is whether the 95% confidence interval (CI) for its coefficient excludes zero (Hosmer and Lemeshow 2000). The 95% CI for habitat excluded zero in all the best candidate models (Table 3), providing strong evidence that habitat affiliation affected rates of species classification. The 95% CI for species assignment excluded zero in two models indicating, along with the positive coefficient, that variation in pelage coloration of meadow voles may have induced lower correct classification rates for the species assignment of montane vole. The 95% CI for age excluded zero in only one of the models, but age was included in all but one of the candidate models suggesting molt may have influenced classification rates. The coefficient associated with year 3 always excluded zero in a 95% CI indicating that experience across field seasons increased the probability of correct species classification. The lower bounds of the 95% CI for week in models without the species*week interaction terms were just below zero indicating that experience within a field season may also have improved classification rates. For sex, the 95% CI included zero, and the fact that sex was included in few candidate models provides inconclusive evidence that pelage color associated with sex affected species classification rates. The 95% CI for the species assignment*week interaction term overlapped zero by a large amount, thus providing weak evidence that classification of

59

individuals termed montane voles improved over time versus individuals termed meadow voles.

Discussion

An accuracy rate of 92% shows that differentiation of meadow and montane voles based solely upon pelage color is possible. Correct classification probabilities based solely on pelage coloration (95% for species assignments of meadow vole and 88% for species assignments of montane voles) showed that species differentiation is possible using this criterion. Although accuracy rates of 88-95% may be acceptable for population-level studies, they may be too low for behavioral studies (Bruseo et al. 1999). Attaining overall accuracy rates greater than 95% would require adjusting for variation in classification probability induced by factors such as habitat, time, age, and species.

In this study, classification probability was significantly lower in grazed than in ungrazed habitat. Light pelage color may confer an advantage to voles in grazed habitat, where low vegetative cover and light colored soil predominate. Generally, meadow voles are darker than montane voles, but this relationship may be inconsistent in low-cover areas: 35% of positively identified meadow voles trapped in grazed habitat exhibited abnormally light pelage coloration versus 5% in ungrazed habitat. This apparently adaptive variation in pelage color can certainly influence classification rates of species. Montane voles are more prevalent in shorter vegetation than meadow voles (Grant et al. 1982, Runge 2005b, D. Christian unpublished data), thus increased cryptic variation by meadow voles in these areas may strongly confound species-specific attributes.

Classification probabilities tended to increase both within and across field seasons, indicating that observer experience can affect classification rate. Juveniles of

60

the two species tended to be more cryptic than adults and consequently were more difficult to classify. Meadow voles exhibit more variation in pelage color than montane voles (Foresman 2001), and thus a species assignment of montane vole was more apt to be incorrect than a species assignment of meadow vole (in ungrazed as well as in grazed habitat). Adjusting for these sources of variation with training before initiation of field research would certainly increase classification rates.

A method exists for differentiating live specimens of the two species in which a researcher must coerce a vole to leave clear molar indentations in modeling clay (Douglass 1976b). The indentations are then analyzed with a microscope to identify individuals to species. Although this method may be impracticable for population-level studies in which many individuals need to be processed in a short time, it may be feasible for behavioral studies in which fewer individuals are studied more intensely. The use of a color spectrometer in a controlled environment offers a more objective analysis of color as related to species identification (Endler 1990), but again, may be difficult to implement for studies needing to process many individuals in a short time. Future studies may be able to differentiate species through genetic analysis (e.g., Conroy and Cook 2000) if adequate funding is available.

Meadow and montane voles in western North America compose an interesting study system in which to investigate the combined effects of competition, predation, and spatial heterogeneity. Key to such investigations is the accurate identification of species. Behavioral studies, which require small sample sizes, may be able to use either genetic samples or molar-indented modeling clay to differentiate species. However, for studies requiring the large number of individuals typically needed to estimate population-level

61

processes such as survival, reproduction, immigration, and emigration, a quick and efficient method such as pelage color assessment is required. Demographic studies can directly incorporate such data into capture-recapture models that include parameters for correct classification probabilities and true species proportions (Runge et al. 2005b). Future studies may improve upon the basic method presented here if researchers conduct a pilot study on species identification in which variation in pelage coloration across age classes, species, and habitats is a primary focus. The key to such a pilot study, and to estimation of correct classification probabilities, is a sample of field-classified animals for which truth (actual species identification) is ascertained. Therefore, ensuring the existence of such a subset of animals will be a vital component of any multispecies study that seeks to incorporate uncertainty in species classification.

Table 1. Candidate models for selecting sources of variation in correct classification probability ordered by AUC from 5-fold cross validation. Category indicates the criterion that included a given model in the candidate set, ΔAICc and ΔBIC indicate the number of AICc and BIC units the model is from the model with the lowest corresponding score, AUC10 and AUC5 are the average areas under the ROC curve for 10- and 5-fold cross-validation for 20 samples, AUC5se is the standard error for the 20 estimates of AUC5, and K is the number of parameters in a given model.

Model	Category	ΔAICc	ΔBIC	AUC10	AUC5	AUC5se	K
spp*week+hab+age+year+sex	AICc	1.54	22.47	0.7044	0.6921	0.0082	9
spp*week+hab+age+year	AICc	0.64	18.02	0.7076	0.6918	0.0099	8
spp+hab+age	Both	1.76	4.79	0.6910	0.6813	0.0101	4
spp+hab	BIC	3.15	2.56	0.6797	0.6792	0.0058	3
spp+week+hab+year	AICc	1.06	11.29	0.6885	0.6784	0.0074	6
spp*week+hab*week+age+year	AICc	1.24	22.17	0.6814	0.6774	0.0086	9
spp+week+hab+age	AICc	1.75	8.39	0.6720	0.6768	0.0036	5
spp+hab+age+year	AICc	1.56	11.80	0.6795	0.6764	0.0089	6
spp+week+hab+age+year	AICc	0.00	13.82	0.6917	0.6718	0.0103	7
spp+week+hab+age+year+sex	AICc	0.69	18.08	0.6818	0.6637	0.0110	8
hab	BIC	4.23	0.00	0.6637	0.6574	0.0141	2
hab+age	BIC	2.55	1.96	0.6318	0.6544	0.0067	3
spp+hab*week+age+year	AICc	1.34	18.72	0.6615	0.6498	0.0116	8
hab+week	BIC	3.76	3.17	0.6397	0.6317	0.0057	3
Global	None	18.63	80.95	0.6109	0.6104	0.0126	21
intercept only	None	17.25	9.37	0.3698	0.4074	0.0105	1

Spp=species assignment, week = week within field season when assignment was made, hab=habitat in which species assignment occurred, age=age of vole at time of species assignment, year=field season in which assignment was made, ld=whether vole was live or dead at time of species assignment

Global model: spp*yr+spp*week+spp*hab+spp*age+hab*week+week*yr+site+sex+ld

Hosmer and Lemeshow's (2000) goodness of fit test (adjusted for expected frequencies less than 5) for global model: $\chi^2 = 1.447$, df = 1, pvalue = 0.229

63

Table 2. Number of individuals assigned to a species (based upon pelage coloration) compared to actual species identification.

		Actual	
		Montane	Meadow
Assigned	Montane	127	17
	Meadow	8	141

64

Table 3. Coefficients (and standard errors) of best models selected by AICc, BIC, AUC5, and AUC10 criteria, and the one model that was a candidate for all four criteria (species assignment+hab+age). For the categorical variables the following factor levels were labeled 1 (as opposed to 0): grazed habitat, meadow vole, adult, female. Thus the coefficient –2.05 for habitat in the 1st model indicates that correct classification probability in grazed habitat is substantially less than in ungrazed habitat.

Model	Habitat	Species est.	Age	Year2	Year3	Week	Sex	Species est.*week
spp*week+hab+age+year+sex	-2.05 (0.54)	0.20 (0.98)	1.15 (0.68)	0.80 (0.56)	1.93 (0.86)	0.13 (0.11)	0.55 (0.50)	0.22 (0.20)
spp*week+hab+age+year	-1.96 (0.53)	0.13 (0.97)	1.24 (0.66)	0.76 (0.56)	1.85 (0.86)	0.11 (0.11)	NA	0.23 (0.20)
spp+week+hab+age+year+sex	-2.03 (0.54)	1.16 (0.54)	1.16 (0.67)	0.81 (0.56)	1.96 (0.87)	0.19 (0.10)	0.58 (0.49)	NA
spp+week+hab+age+year	-1.94 (0.53)	1.15 (0.54)	1.25 (0.66)	0.77 (0.56)	1.87 (0.87)	0.17 (0.09)	NA	NA
spp+hab+age	-1.87 (0.49)	0.83 (0.51)	1.30 (0.65)	NA	NA	NA	NA	NA
hab	-1.85 (0.46)	NA	NA	NA	NA	NA	NA	NA

Spp=species assignment, week = week within field season when assignment was made, hab=habitat in which species assignment occurred, age=age of vole at time of species assignment, year=field season in which assignment was made.

65

Appendix A Chapter 3.

Complete table of models run for the logistic regression examining variables that influenced correct assignment of individuals to species. Spp = species assignment, week = week within field season when assignment was made, hab = habitat in which species assignment occurred, age = age of vole at time of species assignment, year = field season in which assignment was made, site = grid upon which the individual was caught, and ld = whether vole was live or dead at the time of species assignment. ΔAICc and ΔBIC represent the difference in AICc or BIC between the referenced model and the model with the lowest AICc or BIC, and k is the number of parameters in the referenced model.

Model	ΔAICc	ΔBIC	k
spp*year+spp*week+spp*hab+spp*age+hab*week+week*year + site+sex+ld	18.63	80.95	21
spp*year+spp*week+spp*hab+spp*age+hab*week+site+sex +ld	16.17	71.76	19
spp*year+spp*week+spp*age+hab*week+site+sex+ld	13.94	66.14	18
spp*yr+spp*week+spp*age+hab*week+site+sex	12.16	60.95	17
spp*year+spp*week+hab*week+age+site+sex	10.36	55.72	16
spp*week+hab*week+age+year+site+sex	6.30	44.76	14
spp*week+hab*week+site+age+year	5.18	40.17	13
spp+week+hab+age+year+site+sex+ld	7.01	42.00	13
spp+week+hab+age+year+site+sex	5.31	36.81	12
spp*hab+week*year	5.75	26.68	9
spp*week+hab*week+age+year	1.24	22.17	9
spp*week+hab+age+year+sex	1.54	22.47	9
spp+hab*week+age+year	1.34	18.72	8
spp*week+hab+age+year	0.64	18.02	8
spp+week+hab+age+year+sex	0.69	18.08	8
spp+week+hab+age+year	0.00	13.82	7
spp*age+year	13.56	23.80	6
spp*hab+year	5.06	15.30	6
spp*week+year	11.55	21.79	6
spp*year	14.94	25.18	6
spp+hab+age+year	1.56	11.80	6
spp+week+hab+year	1.06	11.29	6
week*year	22.28	32.52	6
spp+hab+year	3.04	9.69	5
spp+week+hab+age	1.75	8.39	5
hab*week	5.06	8.09	4
hab+year	6.04	9.07	4

66

spp*age	15.61	18.64	4
spp*hab	5.18	8.22	4
spp*week	14.88	17.92	4
spp+hab+age	1.76	4.79	4
spp+week+hab	2.81	5.84	4
hab+age	2.55	1.96	3
spp+hab	3.15	2.56	3
year	18.71	18.12	3
hab+week	3.76	3.17	3
age	17.62	13.40	2
hab	4.23	0.00	2
spp	13.10	8.87	2
week	18.35	14.12	2
intercept	17.25	9.37	1

67

Chapter 4. Estimating species-specific survival and movement when species identification is uncertain.

Abstract: The investigation of uncertainty in ecological studies has been the topic of an increasing body of research. In particular, mark-recapture methodology has shown that incorporating uncertainty in the probability of detecting individuals in populations enables accurate estimation of population-level processes such as survival, reproduction, and dispersal. Recent advances in mark-recapture methodology have included estimating population-level processes for biologically important groups despite the misassignment of individuals to these groups. Examples include estimating rates of apparent survival despite less than perfect accuracy when identifying individuals to gender or breeding state. Here we introduce a method for estimating apparent survival and dispersal in species that co-occur but that are difficult to distinguish. We use data from co-occurring populations of meadow voles (*Microtus pennsylvanicus*) and montane voles (*M. montanus*) to show how ignoring species uncertainty can lead to different conclusions regarding population processes. The incorporation of species uncertainty in mark-recapture studies should aid future research investigating ecological concepts such as interspecific competition, niche differentiation, and spatial population dynamics in sibling species.

Key words: mark-recapture methodology, sibling species, spatial population dynamics, niche space, uncertainty, competition.

Introduction

Uncertainty plagues ecological investigations. Quantifying and incorporating this

68

uncertainty into inference procedures has become an increasingly important focus of many research efforts in the past four decades (Seber 1965, Otis et al. 1978, Williams et al. 2002, Clark 2003). The field of statistical ecology has recently begun to recognize that one form of uncertainty, the ability (or lack thereof) to correctly classify individuals to groups such as gender or breeding class, can lead to uncertainty and bias in estimates of vital rates. When this uncertainty is incorporated in statistical methodology for mark-recapture data, vital rates such as survival and reproduction can be accurately estimated for species with cryptic sex or breeding morphologies (Conroy et al. 1999, Lebreton and Pradel 2002, Fujiwara and Caswell 2002, Kendall et al. 2003, Nichols et al. 2004, Pradel 2005). A similar problem occurs when species themselves are difficult to differentiate. Here, we introduce a method for estimating species-specific rates of apparent survival and dispersal when individuals are difficult to identify to species.

Cryptic species co-inhabiting the same area (hereafter "sibling species," *sensu* Futuyma 1998) occur throughout the natural world. For example, many small mammals are sibling species including white-footed mouse (*Peromyscus leucopus*) and deer mouse (*P. maniculatus*), meadow vole (*Microtus pennsylvanicus*) and montane vole (*M. montanus*), and various shrew (*Sorex*) species. Other vertebrate examples include female blue-winged teal (*Anas discors*) and cinnamon teal (*A. cyanoptera*), rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*O. clarki*), *Cnemidophorus* lizards, *Anolis* lizards, and torrent salamanders (*Rhyacotriton*).

Interspecific competition can have a strong impact on the ecology of species (Schoener 1968, Tilman 1999), and the broadly overlapping niche spaces associated with sibling species can intensify competition (although competition can certainly occur

69

among distantly related taxa as well). When one of the sibling species is non-native, the effects of competition may be important for the management and conservation of native species. For instance, introduced rainbow trout may outcompete native cutthroat trout in streams in the American West (Griffith 1988), and invasive mussels from Europe (*Mytilus galloprovincialis*) may be causing a decline of native mussels (*M. trossulus*) in California (Geller 1999). Additionally, investigating how sibling species use adjacent but different habitats may aid in delineating sources (areas where natality outweighs mortality) and sinks (areas where the reverse occurs), a key issue in spatial population dynamics (Kareiva 1990, Dias 1996). One model suggests that source-sink dynamics may allow sibling species to co-exist when otherwise one species would eliminate the other (Schmidt et al. 2000). Thus, investigating how vital rates of sibling species vary with different habitats may advance research concerning the coexistence of similar species. This could have implications for the management and conservation of biodiversity.

Rigorous estimation of differences in species-specific vital rates for sibling species has not yet been investigated. Two elements are crucial for such research. First, individuals must have some morphological characteristic upon which to base field identification of species. Examples include bill shape and size in female teal (LeMaster 1986, Jackson 1991), pelage color in mice (Bruseo et al. 1999, Foresman 2001, Runge *in prep.*), and spotting pattern in trout (Holton and Johnson 1996). Second, an identifier of true species identification must be obtained from a subset of the sampled individuals. Possibly, species-specific vital rates can be estimated using mixture models even when true species cannot be identified with certainty for any animals (e.g., using the models of

70

Pradel 2005), but such models may have identifiability problems in at least some situations. At a minimum, knowledge of true species identity for some individuals permits more precise estimation of quantities of interest.

We note that the method may have broad applicability in that the true identity of sibling species can be determined by a variety of methods. Examples include dental pattern or skull morphology of individuals removed due to pathology research or handling errors, isozymes from blood samples taken from a subset of animals in a combined demographic and immunological study, and DNA samples taken from body tissue or feces. A specific example of applicability concerns sibling species of songbirds (e.g., *Empidonax* flycatchers). The USGS Bird Banding Lab currently prohibits banding of individuals that cannot be identified to species. However, if banding was possible, then researchers using the statistical methodology below could remove feathers from cryptic individuals, identify them to species with a DNA-based method, and obtain worthwhile species-specific information regarding both demography and identification.

In this paper, we present a method to estimate species-specific apparent survival and dispersal despite uncertainty in species identification. We apply the method to populations of meadow and montane voles occurring in two habitats and show how incorporating a classification parameter for species identification can lead to different results than those obtained from "naïve" estimates of species identification unadjusted for misidentification.

Methods

Statistical Model

The model we present is an extension to the multistate analogue of the Cormack-

71

Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965), the Arnason-Schwarz model (Arnason 1972, Hestbeck et al. 1991, Brownie et al. 1993, Schwarz et al. 1993, Williams et al. 2002). The extension concerns the incorporation of uncertain species classification in estimating relevant parameters for the model. In this model, animals that are not released (i.e., that die on capture) are positively identified to species, and animals that are released receive only an estimated assignment (hereafter termed 'assignment') for species identification. We define state as a geographic area, although one could also define state as a stage class based upon morphological characters of individuals or a certain stage in a certain geographic area. Six types of parameters define our model with additional species-specific information available from the complement of two of the parameters:

$\phi_{i(u)}^{(v)rs}$ = probability of survival from period i to $i+1$ for individuals of species u, $u \in$

$\{A,B\}$, age v (y = young, a = adult), in state r, $r \in \{1,2\}$ and movement to state s,

$s \in \{1,2\}$,

$p_{i(u)}^{r}$ = probability of recapture in period i for adults of species u in state r,

$\chi_{i(u)}^{r}$ = probability an individual in period i of species u in state r is never detected again

after period i (this can be written as a function of the above transition and survival

probabilities),

$\pi_{i(A)}^{(v)r}$ = probability that an individual of age v that is first captured in period i and state r is

a member of species A,

$1 - \pi_{i(A)}^{(v)r}$ = probability that an individual of age v that is first captured in period i and state

72

r is a member of species *B*,

$\delta_{i(u)}^{(v)r}$ = probability that an individual of species *u*, *u* ∈ {*A,B*}, is correctly assigned to

species *u*, for period *i*, age *v*, state *r* (assigned *u* | *u*),

$1 - \delta_{i(u)}^{(v)r}$ = probability that an individual of species *u*, *u* ∈ {*A,B*}, is incorrectly assigned to

species *z*, *z* ∈ {*A,B*}, for period *i*, age *v*, state *r* (assigned *z* | *u*),

$\eta_{i(u)}^{(v)r}$ = probability that an individual of species *u*, age *v*, in state *r* that is captured in

period *i* survives capture at period *i* to be released.

Note that capture probability is not defined for young animals, because we deal with

conditional (on release) models, and all young animals become adults after one time step

(animals mature in the interval separating successive sampling occasions). We note that

the probability of surviving and dispersing from 1 location to the other is expressed as

$\phi_{i(u)}^{(v)12}$ or $\phi_{i(u)}^{(v)21}$. We can separately estimate the survival and transition probabilities with

$$\phi_{i(u)}^{(v)rs} = S_{i(u)}^{(v)r} \psi_{i(u)}^{(v)rs}$$

where $S_{i(u)}^{(v)r}$ is the probability that an individual of species *u* and age *v* released in state *r*

at sampling period *i* survives and remains in the study system until just before sampling

period *i* + 1, and $\psi_{i(u)}^{(v)rs}$ is the probability of moving from state *r* to state *s*. The

probability of staying within a state (e.g., ψ_i^{11}) does not have to be additionally estimated

because $\sum_s \psi_i^{rs} = 1$. Thus, fidelity to a state can be calculated from the probabilities of

moving to another state. For instance, in the two-state system presented here,

73

$\psi_i^{11} = 1 - \psi_i^{12}$. With the software program developed to implement this model (UNSPP), the parameters δ, η, π, p, S, and ψ are all estimable from mark-recapture data.

The capture history data from which multistate, mark-recapture statistics are estimated have a specific format. For instance, the capture history 102 would indicate that an animal is captured in state 1 during sample period 1, not captured during sample period 2, and captured in state 2 during sample period 3. As additional modifiers to this standard multistate capture history, we use yBAN to indicate that the individual was young when first caught, was found to belong to species B, was assigned to species A at its first capture, and was not released upon its final capture. The probability associated with this particular circumstance (conditional on release in period 1) would be:

P(102_yBAN) =

$$(1 - \pi_{1(A)}^{(y)1}) \eta_{1(B)}^{(y)1} (1 - \delta_{1(B)}^{(y)1})[\phi_{1(B)}^{(y)11}(1 - p_{2(B)}^1)\phi_{2(B)}^{(a)12} + \phi_{1(B)}^{(y)12}(1 - p_{2(B)}^2)\phi_{2(B)}^{(a)22}]p_{3(B)}^2(1 - \eta_{3(B)}^2). \quad (1)$$

The first expression, $(1 - \pi_{1(A)}^{(y)1})$ is the probability that a young animal caught in state 1 during sample period 1 is a member of species B; because there are only two species in this model, we can simply define this probability as the complement of the probability of being species A. The second expression, $\eta_{1(B)}^{(y)1}$, is the probability of release for individuals of species B, age y, captured in state 1 during sample period 1. The next expression, $1 - \delta_{1(B)}^{(y)1}$, is the probability that a young animal of species B was incorrectly assigned to species A during sample period 1 in state 1. The term within the brackets in equation 1 accounts for the fact that we have incomplete knowledge regarding the animal's location between sample periods 1 and 3. Either the animal stayed in state 1 where it was not recaptured in sample period 2, then moved to state 2 prior to sample

74

period 3 ($\phi_{1(B)}^{(y)11}(1-p_{2(B)}^{1})\phi_{2(B)}^{(a)12}$), or it moved to state 2 prior to sample period 2 but was

not recaptured there in period 2 ($\phi_{1(B)}^{(y)12}(1-p_{2(B)}^{2})\phi_{2(B)}^{(a)22}$). Finally, the term, $p_{3(B)}^{2}(1-\eta_{3(B)}^{(a)2})$,

is the probability the animal was recaptured but not released in state 2 during sample

period 3.

If we modify the above capture history so that the animal is released at its last

capture (denoted by a "Y"), and therefore true species is never known (denoted by a

"U"), i.e., capture history 102_yUAY, then we must adjust the above probability

structure by incorporating the possibility that the species was correctly assigned to

species A:

P(102_yUAY) =

$$(1-\pi_{1(A)}^{(y)1})\eta_{1(B)}^{(y)1}(1-\delta_{1(B)}^{(y)1})[\phi_{1(B)}^{(y)11}(1-p_{2(B)}^{1})\phi_{2(B)}^{(a)12}+\phi_{1(B)}^{(y)12}(1-p_{2(B)}^{2})\phi_{2(B)}^{(a)22}]p_{3(B)}^{2}\eta_{3(B)}^{(a)2}+$$

$$\pi_{1(A)}^{(y)1}\eta_{1(A)}^{(y)1}\delta_{1(A)}^{(y)1}[\phi_{1(A)}^{(y)11}(1-p_{2(A)}^{(y)})\phi_{2(A)}^{(a)12}+\phi_{1(A)}^{(y)12}(1-p_{2(A)}^{(a)2})\phi_{2(A)}^{(a)22}]p_{3(A)}^{(a)2}\eta_{3(A)}^{(a)2}. \qquad (2)$$

Expression 2 thus incorporates the uncertainty associated with the possibility that the

animal could belong to either species A or B.

Two other types of histories are possible. An individual may never receive a

species assignment but may receive a positive species identification. For example,

capture history 102_yBUN would have a similar probability statement to (1) but would

have no δ terms associated with it because it never received a species assignment.

Another possibility is an animal that received neither a species assignment nor a true

species identification, e.g., capture history 102_yUUY. The probability statement

associated with such an individual would be similar to (2) but would have no δ terms.

Probabilities such as (1) and (2) can be viewed as multinomial cell probabilities.

75

Together with the observed numbers of individuals exhibiting each capture history, they form a likelihood function from which estimates can be obtained. In this case, the likelihood was coded into program SURVIV (White 1983).

An additional source of information for δ in many studies may be animals from other areas that are not part of the capture-recapture data set undergoing analysis. Examples may include small mammals from other trapping grids, or amphibians sampled in separate areas. If no difference in rates of correct classification are found among areas sampled, then individuals from different areas can be incorporated in the estimation of δ with a binomial likelihood expression where $c_{i(u)}^{(v)r}$ indicates the number of species u that received assignments and were correctly classified at age v, in state r, during sampling period i, and $d_{i(u)}^{(v)r}$ indicates the total number of individuals of species u receiving assignments at age v, in state r, during sampling period i that were subsequently identified to true species. The binomial likelihood expression would then be

$$L(\delta_{i(u)}^{(v)r} \mid c_{i(u)}^{(v)r}, d_{i(u)}^{(v)r}) = \frac{(d_{i(u)}^{(v)r})!}{(c_{i(u)}^{(v)r})!(d_{i(u)}^{(v)r} - c_{i(u)}^{(v)r})!} \delta^{c_{i(u)}^{(v)r}} (1-\delta)^{d_{i(u)}^{(v)r} - c_{i(u)}^{(v)r}}. \tag{3}$$

This likelihood can be multiplied by the more general capture-recapture likelihood, and estimation can be based on the combined data.

The uncertain species model assumes the following: every animal of species u in state r at sampling period i has the same probability of being recaptured (i.e., $p_{i(u)}^{r}$); every marked animal of species u, age v released in state r at sampling period i has the same probability of surviving and moving to state s by sampling period $i + 1$ (i.e., $\phi_{i(u)}^{(v)rs}$); marks specific to individuals are recorded correctly and are not lost or overlooked; all

76

sampling periods are instantaneous (or at least short relative to the interval between them); animals are released immediately after handling; once animals leave the study area, they do not return (or if they do, temporary emigration is random, Kendall et al. 1997); and fates of individuals are independent of one another. These assumptions are standard for multiage, multi-group, multistate mark-recapture models and violations of these assumptions are discussed in depth elsewhere (Williams et al. 2002).

The model and associated software were developed for a specific sampling situation that includes 2 species, 2 states, and 2 ages. The modeling assumes that transitions between states are Markovian, i.e., the probability of an animal occurring in state r during period $i + 1$ is determined solely by the state of the animal during period i, but no earlier. Our data included only one individual that was not released and not identified to species, so we did not account for such capture histories in the modeling, although this possibility could be readily added. We note that the incorporation of time-specific covariates affecting groups of individuals (e.g., weather conditions) is included in the current computer software, but the incorporation of individual covariates (e.g., body mass) would require additional modeling and software development.

The computer software providing estimates and variances of the parameters listed above is available from the Patuxent Wildlife Research Center's Software Archive (http://www.mbr-pwrc.usgs.gov/software/).

Microtus Data

The data analyzed here were collected between June and August 2002 from trapping grids located near Charlo, Montana. The subjects of the capture-recapture data were voles on a single grid, although data collected on voles from other grids were

77

additionally used to estimate classification probabilities, δ. Grids were 100 x 160m in size with traps spaced every 10 m. Each grid was bisected by a livestock fence, and one half of the grid was grazed, the other half ungrazed. Five total grids formed the experiment. The grid we analyze here did not receive the anticipated treatment of grazing during the trapping season. The "grazed" side of the grid had last contained livestock in November 2001, and the "ungrazed" side had last contained a small number of livestock in October 2000. Nonetheless, significant differences in vegetation structure were recorded between the two areas with the ungrazed side containing higher, more dense vegetation and deeper, more extensive vegetative litter (J. Runge *unpubl. data*).

Vegetation mostly consisted of wheatgrass (*Agropyron*), fescue (*Festuca*), and bluegrass (*Poa*) species with some exotic, invasive forbs such as whitetop (*Cardaria draba*) and thistle (*Cirsium* spp.). Trapping was conducted according to the robust design (Pollock 1982), in which several consecutive secondary trapping periods (or "trap nights") compose a single primary trapping period. Intervals between primary trapping periods were three weeks. Four primary periods composed the total study length for the grid analyzed here, and the third primary period consisted of 5 secondary periods whereas the first, second and fourth primary periods consisted of 4 secondary periods. For this data set, we combine the data across secondary periods within a single primary period so that if an animal was captured in any one secondary period, it is considered captured for the primary period. Thus, the integers composing the capture history (0,1,2) denote whether the animal was not captured (0) for a given primary period or the state in which the animal was captured (1,2).

Once caught, animals were marked both with ear tags and clipped toes to ensure

that marks were not lost or misread. Weight, sex, and breeding condition were recorded for each captured animal. The majority of animals also received an assignment for species based upon dorsal pelage color, with meadow voles having darker overall coloration than montane voles; the primary author was solely responsible for species assignments over the course of the study. Animals that died in traps were identified to species based upon upper molar (M^2) pattern; meadow voles have a posterior loop in the M^2 that is absent in montane voles (Foresman 2001). One trap mortality was not identified to species, and this individual's capture history was deleted from the data set analyzed below.

Age was determined by weight, and the criterion separating young from adults was 14.75 g for animals known or estimated to be montane voles and 17.25 g for animals known or estimated to be meadow voles. These criteria are lower than previously used (e.g., Keller and Krebs 1970) because some voles known to be at least 6 weeks old (thus technically subadults) were captured multiple times but were never observed to weigh more than the threshold of Keller and Krebs (1970). All animals identified as young in one primary sampling period gained sufficient weight to be classified as adults in the subsequent period.

Model Selection

We used a data set consisting only of females for model selection and estimation. We did this because program UNSPP currently does not incorporate the variable "gender" for model selection, and previous work shows that gender-specific differences in both apparent survival and dispersal occur in vole populations (Beacham 1979, La Polla and Barrett 1993, Getz et al. 1994, Coffman et al. 2001), which precludes combining males

79

and females in one data set for estimation purposes.

The parameters δ, η, and S can all be modeled to examine whether they varied across time, state, age, or species; whereas π could be modeled only on time, age, and state. We required only a p for adults in our modeling, because young are assumed to become adults over the interval between sample periods, and the population contained only two age classes; thus animals could not be recaptured as young. Potential predictor variables for the parameter ψ included time, age, species, and direction (e.g., from state 1 to state 2 or vice versa). Insufficient data precluded examining how ψ varied with time. Biologically reasonable combinations of variables and interactions between them were considered for each parameter. We note that parameters can be modeled with values changing stochastically, linearly, or parabolically over time. We label the respective variables "time", "time(lin)", and "time^2" while noting that "time(lin)" and "time^2" represent reduced variable models nested within "time".

A preferred method for model selection involves calculating AIC for a full set of pre-defined biologically reasonable models (Akaike 1973, Burnham and Anderson 2002). However, we hypothesized 5 models to be reasonable for modeling δ, 23 for η, 5 for π, 8 for p, 10 for S, and 4 for ψ. A full model selection routine would involve investigating $5*23*5*8*10*4 = 184,000$ combinations, a daunting task. Thus, some form of sequential model selection was needed.

Because δ could strongly influence species-specific estimates of other parameters, it was modeled first. Then η, π, p, S, and ψ were sequentially modeled. For η and π, the lowest AIC model from fitting one parameter was used to fit the *a priori* variable

structures for the subsequent parameter. Then all variable structures with AIC values close to that of the best model for the previous parameter were considered in combination with all structures yielding AIC values close to that of the best model for the subsequent parameter. For p and S, the same process was repeated, but many additional combinations of p and S were considered because the manner in which p was fit strongly affected the fit for S.

Analysis

We conducted two analyses for parameter estimates, one with program UNSPP, the other with program MARK (White and Burnham 1999). The analysis with UNSPP represents a formal incorporation of uncertainty whereas the analysis with MARK treats species assignments for released animals as actual species identifications and thus represents a naive analysis unadjusted for species uncertainty. We compare two sets of results obtained from UNSPP with corresponding results from MARK. The first set of results is generated by the models with the 2 lowest AIC units as determined by program UNSPP. The second set examines differences in estimates of S and ψ when both parameters vary by species and habitat. This constitutes an interesting model for investigating how the incorporation of species uncertainty affects conclusions regarding spatial population dynamics. This latter model appeared to be overparameterized relative to the data, and one consequence of this was a likely error in the estimated variance-covariance matrix, as evidenced by very large standard errors. We thus used a bootstrap approach to obtain standard errors under this model. Specifically, we selected capture histories with replacement from the original data set, obtaining a new replicate data set at each iteration. We fit the model to each data set and recorded parameter estimates for

81

each data set that showed no evidence of convergence problems. We generated data sets until we obtained 500 such runs. We then computed the standard error of resulting parameter estimates as the replication-based standard deviation of the 500 estimates of each parameter of interest.

Hypotheses

The preferred habitat for both meadow and montane voles is grassland with large amounts of vegetative cover (Getz 1985). For both species we expected S to be higher in ungrazed habitat. Whether montane or meadow vole is the superior competitor in optimal habitat is uncertain (Koplin and Hoffmann 1968, Murie 1971, Hodgson 1972, Stoecker 1972, Douglass 1976). However, all researchers familiar with the two species agree that montane voles more readily select low-cover habitat than meadow voles. Thus, we expected π to be higher in grazed habitat. The same reasoning, along with the fact that the lighter-pelaged montane vole may experience less avian predation in low-cover grazed habitat, led us to predict that S would be higher for montane voles than for meadow voles in grazed habitat.

Source-sink theory (Pulliam 1988) suggests that populations in inferior habitat experience increased immigration and decreased survival and reproduction. If grazed habitat acted as a sink for either species, we expected movement from ungrazed to grazed habitat to be higher than movement from grazed to ungrazed habitat and apparent survival to be higher in ungrazed habitat. Conversely, the theories of balanced dispersal (McPeek and Holt 1992) and unbalanced dispersal (Lin and Batzli 2001, Senar et al. 2002) suggest that movement would be greatest from grazed to ungrazed areas. Balanced dispersal predicts that equal numbers of individuals move between habitats. With

82

numbers of both species much greater in ungrazed than grazed habitat, equal numbers of dispersing individuals between habitats would have resulted in ψ from grazed to ungrazed habitat being greater than vice versa. We note that we cannot conclude whether the system exhibits source-sink, balanced, or unbalanced dispersal dynamics without an estimate of *in situ* recruitment, but our estimates of S and ψ provide some inference regarding the type of spatial population dynamics that occurred across habitats.

Because the data analyzed here were recorded in the first field season of the experiment, we fit models in which p increased linearly through time to test the hypothesis that field workers' ability to set traps correctly and locate vole runways increased as the field season progressed. We expected η either to increase linearly through time as nights became warmer and fewer trap deaths occurred or to increase and then decrease if cold nights in the final trapping session induced more trap deaths.

Results

The model with the lowest AIC was δ (age) η (state+time^2) π (state+age) p (.) S (species) ψ(.). The next closest model was 0.06 AIC units higher and differed only in S being modeled by state. Thirteen additional models were between 0.83 and 1.98 AIC units higher (Table 1, see Appendix A for complete model selection results). The model investigating species and habitat-specific differences in S and ψ (hereafter the "spatial-species model") was 5.18 AIC units higher than the best statistical model, and a model with constancy across all parameters was 88.07 AIC units higher.

For the best statistical model, $\hat{\delta}$ was 0.587 (SE = 0.152) for young and 0.871 (0.038) for adults. As mentioned above, data from both sexes were combined for the

83

estimation of classification probability, whereas all other parameter estimates are for females only. The estimate of p from this model was 0.517 (0.146).

In the model with the lowest AIC, in which S was fit by species, differences in estimates of S between the uncertain species analysis and naive analysis were more apparent than in the model with the second lowest AIC, in which S was fit by state. Estimates of S diverged by 0.089-0.162 (11.0 - 43.2%) for the model in which S was fit by species and 0.030-0.038 (3.7 - 8.5%) when S was fit by state (Tables 2 and 3). Estimates of ψ, however, were identical and indeed this was not surprising in models without species-specific movement (Tables 2 and 3). For the spatial-species model, differences between the two analyses ranged from 0.002 (0.2%) ($\hat{S}$ for meadow voles in ungrazed habitat) to 0.21 (33.2%) ($\hat{S}$ for meadow voles in ungrazed habitat) (Table 4).

Incorporating uncertainty in species misclassification caused higher standard errors for parameter estimates of S and ψ. With the two best statistical models, the standard errors for $\hat{S}$ were an average of 0.048 (34.0%) smaller for the naïve analysis than for the uncertain species analysis (Tables 2 and 3). The same pattern held for the spatial-species model, with standard errors for $\hat{S}$ an average of 0.036 (13.3%) smaller for the naïve analysis than for the uncertain species analysis (Table 4). Similarly, average standard error for ψ was 0.050 (40.4%) smaller in the naïve analysis across all models (Tables 2-4).

We report demographic results from the uncertain species analysis. For the spatial-species model, $\hat{S}$ was higher in ungrazed than in grazed habitat for both species (Table 4). Estimates of S for meadow voles were 0.805 (SE = 0.081) in ungrazed habitat

84

and 0.633 (0.246) in grazed habitat. Estimates of S for montane voles were 0.789 (0.244) in ungrazed habitat and 0.392 (0.116) in grazed habitat, both lower than for meadow voles. The estimated probability of a young individual being a montane vole ($\hat{\pi}$) was 0.383 (0.179) in ungrazed habitat and 0.945 (0.097) in grazed habitat. Similarly $\hat{\pi}$ was 0.152 (0.042) in ungrazed habitat for adults and 0.843 (0.062) in grazed habitat.

For meadow voles, the estimate of ψ was higher from grazed to ungrazed habitat, 0.195 (0.208), than vice versa, 0.019 (0.021). The single estimate of ψ available for montane voles was 0.195 (0.183) for individuals moving from ungrazed to grazed habitat. No female montane voles were observed to move from grazed to ungrazed habitat; thus, this parameter was set to 0.

Discussion

Species identification problems occur throughout various taxa, and here we have presented a method for incorporating species uncertainty when estimating probabilities of survival and dispersal in mark-recapture studies. This adds to the growing literature investigating group uncertainty that includes mis-assignment of individuals to genotype (Lukacs and Burnham 2005) and state (Lebreton and Pradel 2002, Fujiwara and Caswell 2002, Pradel 2005), including the special cases of gender (Conroy et al. 1999, Nichols et al. 2004) and breeding state (Kendall et al. 2003). The inclusion of group classification parameters in mark-recapture methodology provides additional realism and properly incorporates uncertainty in species identification when estimating population level processes.

The analysis of female *Microtus* showed that $\hat{S}$ for both species was lower in grazed habitat. We note that $\hat{S}$ in this study takes into account individuals that disperse

85

across habitats within the sample space but not those that emigrate from the sample space, thus it represents a combination of site fidelity and survival. The large difference between the estimates, 0.81 in ungrazed habitat and 0.44 in grazed habitat (Table 3), suggests that voles in high cover habitat exhibit higher philopatry and survival than voles in low-cover habitat. Therefore, high cover habitat appears to be more valuable for populations of meadow and montane voles. The spatial-species model elucidated species-specific patterns across habitats, with meadow voles having higher estimates of S in both habitats (Table 4). This may indicate that meadow voles are better competitors than montane voles, but more information on predation rates and habitat conditions relative to each species would have to be incorporated to make any conclusions. For both species, $\hat{S}$ was high in ungrazed areas (0.79 for montane voles and 0.81 for meadow voles, Table 4). In grazed areas, $\hat{S}$ was much lower for montane voles (0.39) and slightly lower for meadow voles (0.63). This provides weak evidence that grazed areas act as sinks for montane voles but not for meadow voles. Supporting this conclusion is the observation that no montane voles dispersed from grazed to ungrazed habitat, but the estimate in the reverse direction was 0.20, suggesting that dispersal from ungrazed habitat may support populations in grazed habitat. For meadow voles, $\hat{\psi}$ was 0.02 from ungrazed to grazed habitat and 0.20 from grazed to ungrazed. Whether this indicates a pattern of balanced or unbalanced dispersal depends on the number of individuals dispersing, a metric we cannot obtain without estimating abundance of each species in each habitat. However, this pattern suggests that grazing does not induce source-sink conditions for meadow voles, although we note that both high standard errors for some of the estimates reported above (Table 4) and the lack of an estimate for *in situ* recruitment

86

render our analysis of spatial population dynamics inconclusive.

Correct inference for the analysis of survival rates rests upon the accurate estimation of survival and its standard error. We expect the species-specific parameter estimates in an analysis incorporating species uncertainty to be unbiased, whereas the species-specific estimates of p, S, and ψ in a naïve analysis are potentially confounded by inherent uncertainty in species identification. In this study, the probability of correctly assigning an individual to species was high for adults (the predominant cohort), and species generally exhibited similar survival and movement rates, thus the point estimates from the naïve analysis were included in 95% confidence intervals for estimates from the uncertain species analysis (Tables 2-4). However, if either the probability of correct species assignment was low or survival and movement rates were greatly different between species, then we would expect corresponding parameter estimates to become increasingly biased.

Naïve analyses that do not incorporate species classification uncertainty in systems with sibling species may produce estimates of standard error that are biased low. For six of the eight estimates of S presented here (Tables 2-4), the naïve analysis generated lower estimated standard errors than the uncertain species analysis. Thus, the use of naïve analyses could suggest differences between species that may not be supported when uncertainty in species identification is considered. This could lead to spurious results when investigating ecological processes that differ among sibling species. Conversely, we can make rigorous advances in knowledge of ecological processes such as interspecific competition and preferred niche space among sibling species by incorporating the uncertain assignment of individuals to species. Biased

87

estimation of standard errors in naïve analyses may additionally induce problems with model selection. With standard errors biased low, model selection routines may select higher order models than necessary. This could lead to overfitting and spurious conclusions or to mistaken confidence in a 'best' statistical model. For instance, ΔAIC for the top two models in the unknown species analysis was 0.06 with the model with S varying by species being lower than the model with S varying by state. In contrast, the model with S varying by species in the naive analysis was 9.33 AIC units *higher* than the model with S varying by state.

We note that the current model contains rather specific assumptions about the system of interest, e.g., there are only 2 states, 2 species, and 2 age classes, and all individuals that are not released should be unequivocally identified to species. The details provided here should enable researchers to relax these assumptions in future studies. We foresee that studies using genetic methods to identify individuals to species may identify a sub-sample of individuals in the study but also release these individuals. If so, an extra parameter incorporating the probability of an individual being identified to species, whether it was released or not, would need to be included in the likelihood. If a known percentage of individuals were to be sampled with such a method, then the extra parameter could be fixed to the corresponding probabilistic value.

The coexistence of sibling species is a specific, yet interesting, phenomenon. In some situations, sibling species may represent a recent evolutionary divergence, but they also have the capacity to co-exist in perpetuity (Gurney and Nisbet 1998, Zhang et al. 2004). Additionally, competition between sibling species may have implications for management and conservation of native species (Griffith 1988, Geller 1999).

88

Incorporating uncertainty in species classification should aid researchers investigating these issues. Unfortunately, increases in estimates of standard error for population processes will make the determination of species-level differences more difficult than in systems where species identity is certain. However, ignoring species uncertainty can lead to spurious conclusions regarding ecological theories such as competition and spatial population dynamics and may advance unwarranted conservation and management actions. Therefore, the incorporation of species uncertainty should aid both effective implementation of ecological management and accurate advancement of ecological theory for sibling species.

Table 1. Model selection results. Models shown here are < 2.0 AIC units of the model with the lowest AIC. Parameters as defined in text. k is the number of parameters in a given model, and ΔAIC is the difference between the detailed model and the model with the lowest AIC. sp = species, st = state (habitat), dir = direction specific movement, seas = season, time(lin) indicates the parameter was modeled as a linear function of time, and time^2 indicates the parameter was modeled as a parabolic function of time.

δ	η	π	P	S	ψ	k	ΔAIC
age	st+time^2	st+age	.	sp	.	13	0.00
age	st+time^2	st+age	.	st	.	13	0.06
age	st+time^2	st+age	sp	sp	.	14	0.83
age	st+time^2	st*age	.	st	.	14	1.02
age	st+time^2	st+age	.	sp+st	.	14	1.07
age	st+time^2	st+age	time(lin)	sp	.	14	1.10
age	st+time^2	st+age	time(lin)	st	.	14	1.29
age	st+time^2	st+age	.	sp	sp	14	1.33
age	st+time^2	st+age	st	sp	.	14	1.42
age	st+time^2	st+age	.	sp*seas	.	15	1.52
age	st+time^2	st+age	.	sp	dir	14	1.73
age	st+time^2	st+age	.	st	sp*dir	16	1.80
age	st+time^2	st+age	sp	sp	sp	15	1.83
age	st+time^2	st*age	.	sp	.	14	1.97
age	st+time^2	st+age	sp	st	.	14	1.98

90

Table 2. Parameter estimates (and standard errors) for the best statistical model for meadow voles ("MiPe") and montane voles ("MiMo") using both uncertain species ("Unspp") and naïve analyses.

Analysis	ψ	S MiPe	S MiMo
Unspp	0.041 (0.088)	0.812 (0.135)	0.375 (0.155)
Naïve	0.041 (0.023)	0.723 (0.079)	0.537 (0.107)

Table 3. Parameter estimates (and standard errors) for the second best statistical model (ΔAIC = 0.06) using both uncertain species ("Unspp") and naïve analyses. This model differed from best model in having S differ by state rather than species (Table 1).

Analysis	ψ	S ungrazed	S grazed
Unspp	0.043 (0.089)	0.809 (0.134)	0.449 (0.139)
Naïve	0.043 (0.024)	0.779 (0.092)	0.411 (0.094)

91

Table 4. Parameter estimates (and standard errors, obtained using a bootstrap procedure) from spatial-species.model for meadow and montane voles using both uncertain species ("Unspp") and naïve analyses for grazed ("grz") and ungrazed ("ung") habitat.

	meadow vole				montane vole			
Analysis	ψ ung-grz	ψ grz-ung	S ung	S grz	ψ ung-grz	ψ grz-ung	S ung	S grz
Unspp	0.019 (0.021)	0.195 (0.208)	0.805 (0.081)	0.633 (0.246)	0.195 (0.183)	0	0.789 (0.244)	0.392 (0.116)
Naïve	0.023 (0.022)	0.165 (0.155)	0.803 (0.086)	0.423 (0.148)	0.124 (0.116)	0	0.835 (0.188)	0.424 (0.118)

92

Appendix A Chapter 4

Full set of models analyzed. δ is the probability of correct classification, η is the probability of release, π is the probability that an animal is a montane vole, p is the probability of recapture, S is the probability of surviving and staying within the study area, and ψ is the probability of moving between habitats. "age" indicates that a parameter was modeled on differences between adults and young, "sp" indicates a modeled difference in species, "st" indicates state (i.e., habitat), "time" indicates that a parameter was modeled to vary stochastically with time, "time(lin)" indicates a parameter linearly (within the logit term) increasing or decreasing with time, "time^2" indicates a parabolic change with time, time(2nd) was used to denote the modeling of p with the number of secondary capture periods within a primary period, and "dir" was used to denote the modeling of ψ by different rates between habitats. A "*" indicates an interaction effect between terms indicated, a "+" indicates an additive effect, and a "." indicates that a parameter was modeled as constant across all groups and sample periods. "k" is the number of parameters within a given model. Finally ΔAIC is the difference between the model with the lowest AIC and the model specified.

δ	η	π	p	S	ψ	k	ΔAIC
age	st+time^2	st+age	.	sp	.	13	0.00
age	st+time^2	st+age	.	st	.	13	0.06
age	st+time^2	st+age	sp	sp	.	14	0.83
age	st+time^2	st*age	.	st	.	14	1.02
age	st+time^2	st+age	.	sp+st	.	14	1.07
age	st+time^2	st+age	time(lin)	sp	.	14	1.10
age	st+time^2	st+age	time(lin)	st	.	14	1.29
age	st+time^2	st+age	.	sp	sp	14	1.33
age	st+time^2	st+age	st	sp	.	14	1.42
age	st+time^2	st+age	.	sp*seas	.	15	1.52
age	st+time^2	st+age	.	sp	dir	14	1.73
age	st+time^2	st+age	.	st	sp_dir	16	1.80
age	st+time^2	st+age	sp	sp	sp	15	1.83
age	st+time^2	st*age	.	sp	.	14	1.97
age	st+time^2	st+age	sp	st	.	14	1.98
age	st+time^2	st+age	st	st	.	14	2.00
age	st+time^2	st+age	.	st	sp	14	2.03
age	st+time^2	st+age	time(lin)	st+st	.	15	2.24
age	st+time^2	st+age	st	sp*seas	.	16	2.37
age	st+time^2	st+age	st+time(lin)	sp	.	15	2.53
age	st+time^2	st+age	sp	sp*seas	.	16	2.64
age	st+time^2	st+age	sp	sp+st	.	15	2.66
age	st+time^2	st+age	time(lin)	sp*seas	.	16	2.67
age	st+time^2	st+age	st	.	.	13	2.77
age	st+time^2	st*age	sp	sp	.	15	2.80
age	st+time^2	st+age	.	sp	sp_dir	16	2.91
age	st+time^2	st+age	st	sp+st	.	15	2.98

93

age	st+time^2	st+age		sp*st		15	3.01
age	st+time^2	st+age	st+time(lin)	st		15	3.23
age	st+time^2	st+age		st	dir	14	3.33
age	st+time^2	st*age	st			14	3.72
age	st+time^2	st+age	st+time(lin)	sp*seas		17	3.79
age	st+time^2	st+age	st+time(lin)			17	4.04
age	st+time^2	st+age	st+time(lin)	sp+st		16	4.14
age	st+time^2	st+age	time(lin)	sp*st		16	4.19
age	st+time^2	st+age	sp			13	4.20
age	st+time^2	st+age	sp+st			14	4.43
age	st+time^2	st+age	sp	sp	sp*dir	17	4.48
age	st+time^2	st+age	st	seas		14	4.60
age	st+time^2	st+age	sp*st			15	4.72
age	st+time^2	st+age	st	age		14	4.72
age	st+time^2	st+age	st	sp+st+age		16	4.86
age	st+time^2	st+age	st	sp*st		16	4.91
age	st+time^2	st+age	sp+time(lin)			17	5.03
age	st+time^2	st+age		sp*st	sp*dir	18	5.18
age	st+time^2	st+age	st*time(lin)			18	5.98
age	st+time^2	st+age	sp	sp	dir	15	6.18
age	st+time^2	st+age	st	sp*st+age		17	6.80
age	st+time^2	st+age	sp*time(lin)			18	6.98
age	st+time^2	st+age				12	8.48
age	st+time^2	st+age	time(lin)			13	9.33
age	st+time^2	st*age				13	9.44
age	st+time^2	st				11	12.88
age	st+time	st+age				13	13.63
age	st+time^2	age				11	42.99
age	st+time^2					10	61.71
age	st+time					11	62.65
age	st*seas					10	64.65
age	st*time^2					12	65.66
age	sp*seas					10	66.05
age	sp*time^2					12	66.88
age	sp+time^2					10	66.98
age	st+time(lin)					9	67.56
age	time^2					9	67.67
age	sp+time					11	67.87
age	st*time					14	68.36
age	seas					8	68.44
age	time					10	68.72
age	sp*time					14	69.53
age	sp*time(lin)					10	70.81
age	sp+time(lin)					9	72.43
age	time(lin)					8	73.15

94

age	sp*age					10	78.79
age	sp+age					9	79.82
age	st					8	80.67
age	sp*st					10	80.80
age	sp+st					9	81.44
age	age					8	82.83
age	sp					8	83.79
age						7	86.58
						6	88.07
sp+age						8	88.18
sp						7	88.94
age	st*time(lin)					10	89.51

95

Chapter 5. Spatial population dynamics of *Microtus* in grazed and ungrazed grasslands

Abstract: The quality of a habitat has implications for hierarchical levels of ecology ranging from the gene to the ecosystem. The theory of spatial population dynamics in relation to habitat quality has developed rapidly, and empirical applications of theory have followed suit. One approach to habitat quality uses the population processes of reproduction, survival, and dispersal to categorize habitats according to whether they are sources or sinks while also allowing alternative models such as balanced and reciprocating dispersal. This approach has become popular because it defines habitat quality according to evolutionarily important processes, thus maintaining the broad applicability of the concept. Although empirical applications of the theoretical approach are common, concrete connections between spatial theory and specific land-management actions have yet to be forged. However, management actions can spatially restructure populations and alter the trajectory of natural population dynamics. Therefore, investigations into the effects of management actions on spatial structure should aid understanding of how spatial population theory can be integrated with land management.

Here, I investigate how the common anthropogenic disturbance of livestock grazing affects the spatial structure of populations of montane and meadow voles (*Microtus montanus* and *M. pennsylvanicus*). Four trapping grids were sampled for 3 years in western Montana to determine if livestock grazing induced source-sink, balanced dispersal, unbalanced dispersal, or reciprocating dispersal in vole populations.

Both apparent survival (i.e., combined fidelity and survival) and reproduction were lower in grazed than ungrazed habitats for the two *Microtus* species, and dispersal

96

generally flowed from ungrazed to grazed habitats during 3 years of a population cycle. These patterns suggested source-sink dynamics occurred. However, further investigation raised the possibility that spatial dynamics fluctuated between source-sink and source-source as livestock entered and left grazed areas. This study shows that land managers can exert control over spatial dynamics of focal species. Specifically, the removal of vegetative cover can profoundly affect the structure of vole populations.

Key words: spatial population dynamics, source-sink, balanced dispersal, reciprocating dispersal, habitat quality, dispersal, *Microtus*, land management, livestock grazing, biodiversity, anthropogenic disturbance.

Introduction

Habitat quality strongly influences population dynamics, and differences in quality among multiple habitats can affect the dynamics and persistence of multi-site populations (Birney et al. 1976, Pulliam 1988, Kareiva 1990, Donovan et al. 1995). Many species use multiple habitats, thus the quality of habitats across multiple sites is a global trait of critical importance for management and conservation purposes.

The estimation of reproduction, survival, and emigration is crucial for identifying habitat quality (Runge et al. 2005a). Previous theoretical work has used these processes to categorize local populations in terms of habitat quality and demonstrated that site-specific dynamics together with inter-site dispersal have the potential to strongly influence the dynamics of an entire multi-site population (e.g., Holt 1984, Pulliam 1988,

97

McPeek and Holt 1992, Doncaster et al. 1997, Morris et al. 2004). Although the multi-site approach to population dynamics has been widely applied in conservation settings (e.g., Donovan et al. 1995), little work has been done to test whether manipulation of habitat quality generated by management activities fundamentally alters the dynamics of populations across space (but see Griffin 2004). Here I investigate how a common management tool, livestock grazing, affects populations of voles (*Microtus*). Following the general theoretical and empirical method (Dias 1996, Diffendorfer 1998, Runge et al. 2005a), I categorize habitats according to whether they exhibit spatial dynamics characterized as source-sink, balanced dispersal, unbalanced dispersal, or reciprocating dispersal dynamics.

Source-sink dynamics occur when natality exceeds mortality in superior habitat (source), mortality exceeds natality in inferior habitat (sink), and overall population dispersal flows from source to sink (Lidicker 1975, Hansson 1977, Shmida and Ellner 1984, Holt 1984, Holt 1985, Roughgarden and Iwasa 1985, Pulliam 1988). Balanced dispersal dynamics occur when natality exceeds mortality in both superior and inferior habitats, and emigration rates vary inversely with carrying capacity, leading to population equilibrium and equal numbers of individuals dispersing between habitats (McPeek and Holt 1992, Doncaster et al. 1997, Lemel et al. 1997). Unbalanced dispersal dynamics occur when vital rate patterns are similar to balanced dispersal dynamics, but net dispersal flows from sub-optimal to optimal areas because individuals prefer optimal habitat (Lin and Batzli 2001, Senar et al. 2002). Reciprocating dispersal occurs when dispersal flows from optimal to sub-optimal habitat during times of increasing and peak abundance in the optimal habitat and in the reverse direction during times of decreasing

98

and low abundance (Morris et al. 2004). Thus, the first three categories can all occur through time under the framework of reciprocating dispersal.

Members of the order Rodentia have been used frequently in studies involving spatial population dynamics. Of 143 studies that empirically investigated source-sink, balanced dispersal, or unbalanced dynamics from 1981-2001, 51 (36%) used rodents as a model organism (Runge et al. 2005a), presumably because spatial differences in population processes of rodents are easier to quantify than in most other taxa.

At peak abundances, arvicoline rodents (voles and lemmings) are strongly-interacting species (*sensu* Power et al. 1996) in virtually every ecosystem they inhabit. Their abundance affects the abundance of many predators including raptors (Korpimaki and Norrdahl 1989) and mustelids (Korpimaki et al. 1991, Oksanen and Henttonen 1996), among others. Granivory by voles can drastically alter plant communities (Ostfeld et al. 1997, Howe and Brown 2001, Manson et al. 2001, Howe et al. 2002), and potentially prevent the reestablishment of native grasslands (Bard et al. 2004). Voles also disturb soil, enabling forbs to invade grasslands (Noy-Meir 1988, Bergeron and Jodoin 1993, Milton et al. 1997) and can cause extensive damage to agricultural crops (Getz 1985). Thus, voles strongly affect the diversity and abundance of both plants and animals.

When voles encounter two adjacent habitats with differing amounts of vegetative cover, they tend to establish home ranges in the habitat with more cover (Birney et al. 1976, Grant et al. 1982, Dickman and Doncaster 1987, Kotler et al. 1988, Peles and Barrett 1996, Lin and Batzli 2001), perhaps because cover provides protection from avian predation (Koivunen et al. 1996, Wolff et al. 1999). Livestock grazing effectively reduces vegetative cover and can negatively affect many taxa (e.g., Kirsch 1969, Grant et

99

al. 1982, Shepard et al. 1997, Homyack and Giuliano 2002, Fondell and Ball 2004), yet is commonly used as a tool by land managers and as an economic resource in the American West. Here, I investigate the effects of livestock grazing on spatial population dynamics of montane voles (*Microtus montanus*) and meadow voles (*M. pennsylvanicus*) in western Montana.

In many inter-Rocky Mountain valleys, montane and meadow voles co-occur and, because they are difficult to differentiate, can be defined as sibling species (Futuyuma 1998). Previous evidence suggests that meadow voles prefer wetter habitat than montane voles (Findley 1951, Hodgson 1972) and that both species prefer high vegetative cover (Hodgson 1972, Gaines 1985), although montane voles occasionally are found in habitat with low cover (Hodgson 1972, Grant et al. 1982). Nevertheless, low cover habitat tends to be sub-optimal for most vole species (Birney et al. 1976, Lin and Batzli 2001, Getz et al. 2005). Whether these areas function as sinks or sources for voles remains untested in natural populations, although experimental research on vole populations in fenced enclosures suggests that both balanced and unbalanced dispersal may occur between high and low cover habitats (Lin and Batzli 2001).

Vole populations in the study area appear to be cyclic with a period of 3-5 years (D. Christian pers. comm.), and variation in habitat quality at the landscape level has the potential to influence population cycles of microtines (Lidicker 1975, Birney et al. 1976), as well as other small mammals (Howell 1923, Dolbeer and Clark 1975, Wolff 1980, Keith et al. 1993). Varying levels of abundance through three years of a population cycle allow for a critical investigation of density-dependent dispersal. Coupled with estimates of habitat quality, this allows for the delineation of models that exhibit differing patterns

100

of density-dependent and density-independent dispersal (e.g., source-sink, reciprocating dispersal, etc.).

In this paper, I examine patterns of abundance in montane and meadow voles and investigate which population processes most affect abundance in different habitats. I then attempt to determine the type of spatial population dynamics that grazing induces by investigating patterns of directional dispersal during three years of a population cycle. Within the context of spatial population dynamics, I also investigate the vegetation attributes that influence habitat quality for these two, closely related species.

Hypotheses

The overarching hypothesis of this study is that livestock grazing induces spatial structure in vole populations by reducing survival and/or reproduction. Investigation of the type of spatial structure leads to a set of competing subsidiary hypotheses: grazing could induce source-sink, balanced dispersal, unbalanced dispersal, or reciprocating dispersal dynamics. To investigate which of these models operate through a population cycle, I examine differences in survival, reproduction, and dispersal between habitats. A metric combining survival, reproduction, and emigration is used to estimate the contribution a population in one habitat makes to the overall, multi-habitat population (Runge et al. 2005a). If source-sink dynamics occur throughout a population cycle, the contributions of grazed habitats should be consistently less than ungrazed habitats during each phase of the cycle, and dispersal should occur primarily from ungrazed to grazed habitat. If unbalanced or balanced dispersal occurs throughout a population cycle, contributions should be roughly equal between habitats. However, the number of individuals dispersing from grazed to ungrazed habitat should exceed those dispersing in

101

the opposite direction if unbalanced dispersal occurs, whereas the numbers of individuals dispersing between habitats should be roughly equal if balanced dispersal occurs. If reciprocating dispersal is the dominant paradigm, differences in contributions between habitats should vary throughout a cycle, and directional dispersal should depend upon fluctuating densities in the optimal habitat rather than exhibit a consistent pattern.

The investigation of vital rates in a given habitat type provides inference regarding the type of spatial population dynamics that occurs, but an issue of deeper importance for a land manager concerns the type of vegetation structure that most affects population dynamics of voles. Previous evidence suggests that meadow voles prefer areas with more forbs than grasses (Getz 1985, but see Getz 2005). Additionally, many landowners in the Mission Valley view reduction of litter cover as an effective means for reducing vole abundance, thus the amount of cover may affect survival and abundance of both species. Correspondingly, I examine the types of vegetation structure that affect population dynamics of voles and investigate how the manipulation of vegetation structure can affect the spatial structure of vole populations.

Methods

In this section I first detail the study area, and then discuss details related to trapping and handling of voles including spatial and temporal aspects of the experimental design. Next I explain the vegetation metrics used as predictor variables in statistical analyses and then describe the statistical methodology used. This final section includes a brief summary of the problem induced by uncertain species identification, a method for deriving species-specific abundance given this uncertainty, a summary of the criterion

102

used to differentiate sources and sinks, and, finally, details of the statistical analyses used.

Study area

The study area consisted of five trapping grids in the Mission Valley of western Montana at an altitude of 900 m. Land in the valley is typically grazed, mowed for hay, or planted for wildlife food and cover. Grazed areas are planted with a variety of exotic grasses and legumes. Ungrazed areas mostly consist of wheatgrass (*Agropyron*), fescue (*Festuca*) and bluegrass (*Poa*) species. Exotic invasive forbs such as whitetop (*Cardaria draba*), mustard (*Brassica spp.*), and thistle (*Cirsium spp.*) are also common.

Trapping protocol

Five sites with adjacent grazed and ungrazed grasslands that contained no features likely to constrain vole dispersal (e.g., ponds, active irrigation ditches, roads) were located, and trapping grids were randomly placed on these sites. Each grid was 1.6 ha and bisected by a fence that excluded livestock from half the grid. One hundred and sixty traps were placed in a 16 x 10 pattern, with 10 m between each trap. Grids were 100 m wide and extended 80 m into grazed grassland and 80 m into ungrazed grassland. Trapping on the sites was conducted from June-August 2002 and May-September 2003-2004 except for one site that was trapped only in 2002 because it did not receive the anticipated treatment of livestock grazing. Grazed habitat contained cattle for 1-4 weeks followed by 1-8 weeks of rest. 'Ungrazed' habitat had been left idle for at least 2 years.

Each overall trapping session (or primary period [Pollock 1982]) was composed of 3-5 secondary periods. These secondary periods generally were one night in length, but secondary periods were conducted during daylight hours in September 2003, May-June 2004, and September 2004 to minimize cold-induced trap mortalities. Intervals

103

between primary trapping periods were three weeks. Each grid was trapped for 2-4 primary periods in 2002 and for 6-7 primary periods in 2003.

Voles were marked both with ear tags and by clipping toes to mitigate tag loss. Weight, sex, and breeding condition were recorded for each vole. The two species occurring in the study area, meadow vole and montane vole, are difficult to differentiate (Hall 1981, Foresman 2001). Meadow voles tend to have darker and redder dorsal pelage coloration than montane voles (Runge 2005), and captured individuals were assigned to species based on this characteristic. Animals that died in traps were identified to species based upon upper molar (M^2) pattern; meadow voles have a posterior loop in the M^2 that is absent in montane voles (Foresman 2001). The combination of confirmed species identification from M^2 pattern and species assignments made in the field allowed for statistically rigorous estimation of species-specific vital rates (Runge et al. 2005b).

Standard measures of breeding condition such as vaginal perforation or descended testes proved to be unreliable for age evaluation. Females weighing 9-10 g were occasionally observed to exhibit vaginal perforation, and several males exhibited both descended and retracted testes over the course of a single handling session (1-2 minutes). Therefore, weight was used to determine age, with 14.75 g separating adults from young for animals known or estimated to be montane voles and 17.25 g for animals known or estimated to be meadow voles. These thresholds were lower than the threshold of 21 g previously used (e.g., Keller and Krebs 1970) because many voles recaptured in primary periods subsequent to the primary period they were first captured were in breeding condition (i.e., pregnant, lactating, or with large, descended testes) but weighed less than 21 g. Thus, the low value of these thresholds minimized the probability that an adult was

104

misclassified as a juvenile and ensured that individuals classified as juveniles were not

immigrants, an assumption crucial to the estimation of *in situ* recruitment (Nichols and

Pollock 1990). However, these thresholds may induce underestimation of *in situ*

recruitment, an issue I discuss below.

Vegetation Measurement

Vegetation height-density was measured at 60 randomly chosen points on each

grid with the Robel (et al. 1970) method. Litter depth and estimated percent litter cover

were measured for a 0.5 m quadrat at a location near the Robel measurement. Litter was

defined as dead vegetation lying horizontal (or nearly so) to the ground. The product of

litter depth and litter cover divided by 100 was used to characterize overall litter structure

(hereafter "litter"). The litter term is best thought of as litter depth in centimeters scaled

by percent coverage. Robel and litter measurements were taken during six primary

periods in 2003 and 2004, and during one primary period in 2002. In the ungrazed

habitat of each grid, % grass, % forb, and % bare ground cover were recorded for a 0.5 m

quadrat on 30 randomly selected points. These measurements were taken once each year.

The same measurements were not taken on the grazed side of each grid because attempts

to separately estimate % grass cover and % forb cover of clover (genus *Trifolium*) proved

inaccurate in areas of extremely low cover. Averages of habitat-specific vegetation

measurements were used as predictor variables in analyses described below.

Statistical Methodology

The general methodology used for the estimation of abundance and vital rates was

capture-mark-recapture (Laplace 1786, Lincoln 1930, Zippen 1956, Cormack 1964). The

experimental and sampling situation suggested a mulistate-robust design estimation

105

procedure (Arnason 1972, Pollock 1982, Pollock et al. 1990, Skvarla et al. 2004) in which the different habitats on each grid represented different states. However, complications arose due to the "uncertain species" aspect of the study. A methodology incorporating both multiple states and uncertain species was derived so that the correct assignment of individuals to species could be rigorously integrated into the estimation procedure (Runge et al. 2005b). This approach precluded likelihood-based estimates of abundance (e.g., Kendall et al. 1995) but allowed for a derived estimate of abundance described below. The statistics and parameters used for estimating abundance and vital rates are described in Table 1.

Estimation of Abundance.—To estimate species-specific abundance for a given primary period, the following statistics were calculated: the number of individuals of known species U that were caught (n_U^*), the number of individuals estimated to be species U that were caught (n_U^{est}), the probability of correctly identifying an individual of species U ($\hat{\delta}_U$), the probability of an individual first caught in a particular primary period being a member of species U ($\hat{\pi}_U$), and the capture probability for a primary period ($\hat{p}^*$). The $\hat{\delta}_U$ and $\hat{\pi}_U$ terms were estimated using program UNSPP (Runge et al. 2005b). Multistate-robust design software were used to estimate p^* for a given primary period; program MARK (White and Burnham 1999) was used when few trap mortalities occurred, and program MSSRVRD (Skvarla et al. 2004) was used when many trap mortalities occurred. MSSRVRD more rigorously accounts for trap mortalities in the estimation of $\hat{p}^*$ using the methods of Yip et al. (2002). Males and females were modeled with the same capture probability because combined-gender models had lower

106

AIC than gender-specific models for 10 of the 12 datasets analyzed (J. Runge, unpublished data).

The number of montane voles (designated species M) and meadow voles (species P) that were caught in a given primary period and received a provisional species assignment but were never positively identified to species ($\hat{n}'_M$ and $\hat{n}'_P$) can be estimated by solving the set of equations

$$\hat{n}'_M \hat{\delta}_M + \hat{n}'_P (1 - \hat{\delta}_P) = n_M^{est}$$
$$\hat{n}'_M (1 - \hat{\delta}_M) + \hat{n}'_P (\hat{\delta}_P) = n_P^{est}$$

(1)

for $\hat{n}'_M$ and $\hat{n}'_P$. Expression (1) states that the number of individuals receiving a provisional species assignment of, for example, M is the sum of two terms: the number of individuals of species M caught and released that were correctly identified, and the number of individuals of species P that were caught and released but incorrectly identified. The $\hat{\delta}_U$ and n_U^{est} terms are known, but the n' terms need to be estimated. The solution for the n' terms is:

$$\begin{bmatrix} \hat{\delta}_M & (1 - \hat{\delta}_M) \\ (1 - \hat{\delta}_P) & \hat{\delta}_P \end{bmatrix}^{-1} \begin{bmatrix} n_M^{est} \\ n_P^{est} \end{bmatrix} = \begin{bmatrix} \hat{n}'_M \\ \hat{n}'_P \end{bmatrix},$$

which was implemented using a program written in MATLAB (Mathworks inc.).

To obtain an estimate of overall species-specific abundance ($\hat{N}_U$), additional adjustments must be made for individuals that never received a provisional species assignment nor were conclusively identified to species (n^{unk}) and for individuals that were identified conclusively (n_U^*). First, n^{unk} is multiplied by the probabilities of an individual being a montane vole ($\hat{\pi}_A$) or a meadow vole ($1 - \hat{\pi}_A$) to assign the n^{unk} individuals to

107

species ($\hat{n}_M^{unk}$ and $\hat{n}_P^{unk}$). Then, the sum of the species-specific terms divided by $\hat{p}*$ determines the species-specific abundance of released individuals,

$$\hat{n}_U^* = \frac{\hat{n}_U^{unk} + \hat{n}_U'}{\hat{p}*}.$$ (2)

Finally the species-specific estimate of abundance for released individuals obtained from equation (2) and the number of unreleased individuals that were identified to species is summed to determine the overall estimate of species-specific abundance,

$$\hat{N}_U = \hat{n}_U^* + n_U^*.$$ (3)

An estimate of variance for $\hat{N}_U$ was not calculated because of the unestimated covariance that occurs among the parameters used to derive $\hat{N}_U$.

Estimates of population growth ($\hat{\lambda}$) were calculated as the abundance of a given species in a given habitat for one primary period divided by the estimate from the previous primary period. If a population estimate in the previous primary period was 0, then $\hat{\lambda}$ was not calculated for that particular interval.

Survival, Dispersal, Reproduction, and Delineation of Sources and Sinks.—Age- and species-specific estimates of abundance in each habitat for each primary period were obtained using the method outlined above. To estimate per capita reproduction of each species ($\hat{\beta}_U$) for a given habitat and primary period, the estimated abundance of young was divided by the estimated abundance of adults. I used both males and females for this metric because gender-specific sample sizes for young were too low to ensure reliable estimates of $\hat{\beta}_U$. The low weight thresholds used to differentiate young and adults may

108

have resulted in estimates of $\hat{\beta}_{ij}$ that were biased low, i.e. some young may have been misclassified as adults. This approach was taken to ensure that bias lay in a known direction; if a higher weight threshold was used, both adults and young may have been mislabeled. Additionally, lower weight thresholds increase the probability that an individual labled as young was produced in the sample area and was not an immigrant, an assumption crucial for calculating per capita local recruitment (Nichols and Pollock 1990).

Species-specific survival ($\hat{S}_{ij}$) and dispersal ($\hat{\psi}_{ij}$) between habitats were estimated using program UNSPP (Runge et al. 2005b). The term for survival actually represents "apparent survival," i.e., the combined probability of surviving and staying in the sample space. Therefore, $\hat{S}_{ij}$ fails to account for individuals that emigrate from the sample space (although it does incorporate dispersal occuring between habitats in the sample space). Data from females only were used for this analysis because program UNSPP currently does not incorporate the variable "gender" for model selection, and previous work shows that gender-specific differences in both apparent survival and dispersal occur in vole populations (Beacham 1979, La Polla and Barrett 1993, Getz et al. 1994, Coffman et al. 2001). Furthermore, female meadow voles distribute themselves according to resources, and males tend to distribute themselves according to the availability of breeding females (Madison 1980). Thus, focusing on females seemed prudent for investigating habitat quality.

The criterion used for differentiating sources and sinks for a given species in a given habitat was denoted C (Runge et al. 2005a) and estimated as

109

$$\hat{C} = \hat{S}_A + \hat{S}_Y \hat{\beta}, \tag{4}$$

where the subscripts A and Y denote adults and young. A habitat is classified as a source if $C \geq 1.0$ and a sink if $C < 1.0$. C represents the contributions a habitat makes to the multisite population if the term for S incorporates emigration. As mentioned above, estimates of S derived from multi-state analyses incorporate estimates of emigration that occurs within the sample space. However, emigration from the sample space will produce estimates of S and C that are biased low. Therefore, a more accurate criterion is

$\hat{C} = \hat{S}_A + \hat{S}_Y \hat{\beta} + \hat{E}_{OSS(A)} + \hat{E}_{OSS(Y)} \hat{\beta}$ where the $\hat{E}_{OSS}$ terms represent survival of those individuals emigrating from the sample space but staying within the multisite population of interest (Runge et al. 2005a). Also note that for this analysis, $\hat{S}$ was estimated using only females, but $\hat{\beta}$ was estimated using both sexes. This assumes that the ratio of juvenile males to adult males is not systematically different than the ratio of juvenile females to adult females.

Sparse data for young hindered estimation of S_Y specific to year, grid, species, and habitat. An analysis that combined young across years and trapping grids was conducted to estimate habitat- and species-specific S. Estimates obtained were generally higher than the estimates of S for adults, which is inconsistent with past research (Eccard and Ylonen 2004, Ozgul et al. 2004). Thus S_Y was assumed to equal S_A.

Estimating S and ψ for sibling species involves the modeling of six different parameters: η (the probability of an individual being released), δ, π, p, S, and ψ (Runge et al. 2005b). Because I was investigating species-specific differences in S between habitats, I tried to fit each parameter by a species*state interaction so that covariance

110

between other parameters and S would be modeled properly. Unfortunately, species*state models failed to converge for many of the datasets. To obtain estimates for S and ψ, I fit η by species, δ by species, π by habitat, and p as a constant. η was additionally fit by season (late spring vs. summer) for 2002 and 2003 data because more trap mortalities occurred in spring during those years. The resulting parameter structure was the most general structure possible across the four grids and three years of the study given problems with sparse data.

Statistical Analyses.—To investigate the specific type of spatial population dynamics that occurred, I examined differences in $\hat{C}$ between habitats for each grid in each year. For each year, I chose the maximum value of $\hat{C}$ (hereafter, $\hat{C}_{max}$) for each grid in each year because this represented the maximum potential contributions of a habitat and thus the maximum level of population fitness. Taking an average for each grid in each year would have led to an estimate based mainly on S, because $\hat{\beta}$ for many primary periods in summer was 0. Two analyses were conducted with this information. First a paired t-test was conducted on the differences between $\hat{C}_{max}$ in grazed and ungrazed habitats. Second, to investigate temporal changes in $\hat{C}_{max}$, each grid received a designation of its cyclic dynamics for a given year (peak, low, or increase) based upon abundance estimates, and this was used as the predictor variable in an ANOVA analysis to investigate whether habitat quality as measured by $\hat{C}_{max}$ changed throughout a cycle. Different analyses were conducted for each species because their temporal population dynamics were not always synchronized, and grid was used as a blocking factor in both of these analyses. Only one population was trapped during a decreasing phase, and this

111

population was grouped with the "low" population category.

I conducted a similar analysis to investigate density-dependent dispersal in montane voles. Very little dispersal was observed for meadow voles, so they were not considered for this type of analysis. Additionally, few montane voles dispersed from grazed to ungrazed habitats, so this analysis tested the timing of dispersal from ungrazed to grazed habitat. Estimates of ψ_M were the response variable in this analysis, cyclic phase was a predictor variables, and grid was a blocking factor. To ensure adequate sample sizes, I analyzed a combined-gender dataset.

To investigate whether grazing induced decreases in S for a given grid in a given year, I fit two models in program UNSPP, one with S different across habitats (designated $S[hab]$), and one with S constant across habitats (designated $S[.]$). I held S constant across time and tested one species at a time. The likelihood ratio χ^2 statistics from each grid in a particular year were given a sign representing whether the difference in survival between habitats was in the direction expected. For each grid, the signed χ^2 statistics were summed across years, then divided by the square root of the number of years a grid was trapped to produce a normally-distributed z statistic for that grid (Everitt 1977, Pradel et al. 1997). The same process was repeated across grids to give a global z statistic for the entire study. This analysis was conducted for females on 10 datasets (grid/year combinations) for montane voles and 6 datasets for meadow voles; analysis of all 12 datasets was not possible due to sparseness of data in grazed habitats.

To investigate whether S was associated with vegetation structure, z statistics were obtained as described above and used to compare the $S[hab]$ model with a model fitting S to either the Robel metric or litter measurements taken in each primary period of

112

a field season. Tests were carried out for montane voles in grazed habitat (insufficient numbers of meadow voles were captured in grazed habitat to test time-specific variables) and for both species in ungrazed habitat. Vegetation variables were incorporated in one column of the design matrix in program UNSPP, thus the difference between $S[hab]$ and the model with S varying by a vegetation measure (hereafter $S[rob]$ or $S[lit]$) was 1 df, and the z-test outlined above could be conducted. Sufficient vegetation and capture history data were available to use 6 datasets (3 grids in 2003 and 2004) for this analysis.

To investigate which elements of vegetation structure affected abundance, I conducted an analysis with % grass cover, % forb cover, % bare ground, Robel, litter, and species as predictor variables and vole abundance during the primary period that vegetation was measured as the response variable. This analysis was conducted only for ungrazed habitats because grass and forb cover were not measured in grazed areas due to inaccuracies in separately estimating % cover for grass and clover (a forb) in low-cover areas. Many of the vegetation variables were highly correlated, so only one vegetation variable was considered in a given model. Because many non-nested models were compared and the goal was to investigate multiple vegetation structures that could affect vole abundance, an information-theoretic approach using the statistical criterion AIC_c (Akaike 1973, Burnham and Anderson 2002) was conducted. For this analysis, a females-only dataset was used.

Patterns of variation in reproduction for *Microtus* have been explained by the existence of the chemical compound 6-MBOA in plants (Berger et al. 1981, Sanders et al. 1981, Korn and Taitt 1987). However, differences in habitat-specific reproductive processes could help to explain habitat quality for meadow and montane voles. I

113

investigated whether reproduction decreased from spring to late summer and how reproduction varied by species and habitat. For this analysis, I used measures of reproduction ($\hat{\beta}$) obtained from each primary period of each grid in each year. To account for covariance on measures of reproduction taken only 3 weeks apart on the same grid, I designated each grid/year combination a "subject", maintained a subject*julian day interaction throughout the model selection process, and tested whether $\hat{\beta}$ varied by species and habitat. I used ANOVA and F tests with $\alpha = 0.05$ for this analysis. A combined-gender dataset was used for this analysis.

Datasets were checked for normality and transformed as needed. If no suitable transformation could be found, non-parametric tests were conducted. All ANOVA, regression, t-test, and non-parametric test procedures were conducted in the programming environment R, version 2.0.0 (R Development Core team 2004) or in SPSS, version 12.

Results

Patterns of Abundance

Populations of both species displayed cyclic tendencies on all grids (Fig. 1). Average abundances across all years, primary periods, and grids for montane voles were 39 (range: 0 - 161) in ungrazed habitat and 16 (range: 0 - 80) in grazed habitat, and for meadow voles 28 (range: 0 - 144) in ungrazed habitat and 4 (range: 0 - 27) in grazed habitat. Estimated population growth ($\hat{\lambda}$) ranged from 0 - 14.6 for montane voles in ungrazed habitat and 0 - 7.5 in grazed habitat, and from 0 - 2.1 for meadow voles in ungrazed habitat and 0 - 3.7 in grazed habitat. Average Pearson correlation coefficients

114

of $\hat{\lambda}$ for a given primary period among grids were 0.49 (range: 0.17 - 0.87) for montane

voles in ungrazed habitat and −0.27 (range: −0.36 - 0.49) for meadow voles in ungrazed

habitat. The average correlation of $\hat{\lambda}$ between meadow and montane voles in ungrazed

habitat on the same grid was −0.21 (range: −0.52 - 0.04). The average correlation of $\hat{\lambda}$

between ungrazed and grazed habitat in the same primary period on the same grid was

0.26 (range: 0.11 − 0.41) for montane voles and 0.54 (range: 0.09 − 0.85) for meadow

voles.

Broad-scale Effects of Grazing

For montane voles, $\hat{C}_{max}$ ranged from 0.11 to 1.43 in ungrazed habitat and from 0

to 1.39 in grazed habitat. For meadow voles, $\hat{C}_{max}$ ranged from 0 to 1.50 in ungrazed

habitat and from 0 to 1.46 in grazed habitat. Despite the overlap in ranges, graphical

analysis suggested that systematic differences in values of $\hat{C}_{max}$ between the two habitats

existed (Fig. 2, Appendix A).

Values of $\hat{C}_{max}$ for the two habitats and two species appeared to be normally

distributed (Kolmogorov-Smirnoff test, N = 12, p = 0.69, 0.877, 0.778, 0.648 for

montane voles in ungrazed and grazed habitat and meadow voles in ungrazed and grazed

habitat), and variances in $\hat{C}_{max}$ for the two habitats were nearly equal for both species,

therefore assumptions for the paired t-test were met. Differences in $\hat{C}_{max}$ between

habitats were significantly different than 0 for montane voles (paired t-test, mean of

difference 0.246; 95% CI: 0.055-0.438) and for meadow voles (mean = 0.346; 95% CI:

0.006-0.686). Thus a difference in quality between the habitats was supported with

115

ungrazed habitat having higher values of $\hat{C}_{max}$.

Apparent survival ($\hat{S}$) was generally higher in ungrazed than grazed habitat, with some exceptions (Table 2, see Appendix A for full results). Average values of $\hat{S}$ across all grids and years were 0.662 for montane voles in ungrazed habitat and 0.527 in grazed habitat, and 0.664 for meadow voles in ungrazed habitat and 0.411 in grazed habitat.

The null hypothesis of no difference in $\hat{S}$ between habitats was rejected in favor of the alternative hypothesis that $\hat{S}$ differed between habitats for montane voles ($z = -3.403$, $p < 0.001$), but not for meadow voles ($z = -0.749$, $p = 0.227$). The statistical tests seem to counter the average values reported above, but note that standard errors for meadow voles in grazed habitat were relatively high due to few releases there (Table 2); thus the power of this test for meadow voles was likely low (Everitt 1977).

Dispersal ($\hat{\psi}$) tended to flow from ungrazed to grazed habitat rather than in the opposite direction (Table 3). Generally, $\hat{\psi}$ ranged from 0.01 - 0.06 with some outliers that were conditioned on few releases. Dispersal rates >0 from grazed to ungrazed habitat for montane vole were similar in value to dispersal rates in the opposite direction. Differences in direction-specific $\hat{\psi}$ were significant for montane voles (Wilcoxan signed ranks, $z = -2.197$, $p = 0.028$). Only one dispersal event occurred from grazed to ungrazed habitat in meadow vole populations, and no statistical tests on differences in direction-specific $\hat{\psi}$ were carried out due to sparse data for meadow voles in grazed habitat.

As expected, per capita reproduction ($\hat{\beta}$) exhibited a tendency to decrease

116

through summer ($F_{26,245} = 40.27$, p < 0.001). No difference in $\hat{\beta}$ between species was

evident ($F_{26,245} = 0.033$, p = 0.855), but the difference in $\hat{\beta}$ between habitats was

statistically significant ($F_{26,245} = 21.383$, p < 0.001). The mean for $\hat{\beta}$ in ungrazed

habitats across the two species and all grids and years was 0.135 in ungrazed habitats

versus a mean of 0.043 in grazed habitats. Maximum rates of $\hat{\beta}$ observed in any single

primary period for montane voles were 0.80 in ungrazed habitat and 0.93 in grazed

habitat and for meadow voles 4.41 in ungrazed habitat and 1.31 in grazed habitat.

Effects of Vegetation Structure

Vegetation height-density (Robel et al. 1971) in grazed habitat significantly

affected $\hat{S}$ for montane voles (z = -1.627, p = 0.047), but insufficient information

precluded conducting the same test for meadow voles. In ungrazed habitat, neither VHD

nor litter appeared to affect $\hat{S}$ for montane voles (VHD: z = 1.768, p = 0.961; litter: z =

0.565, p = 0.714) or meadow voles (VHD: z = -0.227, p = 0.410; litter: z = 1.009, p =

0.844). The average logit coefficient across the six datasets used for this analysis was

4.014 and the average intercept (i.e., the average value of $\hat{S}$ when Robel = 0) was -1.057

(Fig. 3).

In ungrazed habitats, the effect of vegetation structure on $\hat{N}$ was inconclusive.

The model ranked lowest by AIC_c was an intercept-only model. Thus, the vegetation

structure measured may have exhibited little influence on $\hat{N}$. Models within 2.00 AICc

included those fit to % grass cover ($\Delta AIC_c = 0.40$), litter ($\Delta AIC_c = 0.42$), a litter * species

interaction ($\Delta AIC_c = 1.00$), % bare ground ($\Delta AIC_c = 1.73$), and species only ($\Delta AIC_c =$

1.89) (Table 4). I detail the parameter coefficients (and standard errors) as well as the

117

model-based abundance estimate at the lowest vegetation measured for those models within 1.00 AICc of the intercept-only model. The lowest percent grass recorded was 8.3% at which the model predicted an abundance of 7.0 voles. A coefficient of 0.3 (SE = 0.2) indicated that for every 10% increase in grass cover, populations in 0.8 ha of ungrazed habitat would increase by 3 voles. The lowest value of litter was 0.5 at which the model predicted an abundance of 10.6 voles. With a coefficient of 5.8 (4.0), we would expect a probabilistic increase of 5.8 voles for every increment in 1 cm of litter if litter cover was 100% over a 0.8 ha area. The litter*species interaction model suggested that montane voles may respond differently to litter cover than meadow voles. At the minimum level of litter observed in ungrazed areas, the model predicts abundances of 4.8 montane voles and 16.4 meadow voles. The coefficient for litter for montane voles was 13.4 (5.3), indicating that we would expect a probabilistic increase of 13.4 voles for every 1 cm increment in litter cover of 100%. The slope for meadow voles was significantly less; the coefficient for the meadow vole * litter interaction was −15.6 with a standard error of 7.5, suggesting that litter did not affect abundance of meadow voles at the levels measured. This analysis was conducted for ungrazed areas only, and minimum levels of litter found in grazed areas were often 0; thus, extrapolating this model to grazed habitat would be erroneous.

Density Dependence in $\hat{C}_{max}$ and Dispersal

The difference in $\hat{C}_{max}$ between grazed and ungrazed habitats did not change significantly through the phases of the population cycle for either species (montane voles: $F_{5,6} = 1.754$, $p = 0.251$; meadow voles: $F_{5,6} = 0.693$, $p = 0.648$). Similarly, dispersal from ungrazed to grazed habitats for montane voles did not exhibit significant differences

118

throughout the different phases ($F_{5,5} = 4.619$, p = 0.073). The estimated average dispersal was 0.043 during lows, 0.021 during peaks, and 0.008 during increasing phases of abundance.

Discussion

Cyclic Patterns of Abundance and Synchronization of Cycles

Measurements of abundance (Fig. 1) show that vole populations tend to be cyclic in the study area but that patterns are less synchronized than in some other microtine populations (e.g., Ims and Andreassen 2000). Note though that late spring of 2004 could be characterized as a low for most populations sampled (Fig. 1). Extremely high peak years may also be correlated across populations. Such a year occurred in 2005, when vole populations caused many ungrazed grasslands to resemble grasslands grazed by livestock (I. J. Ball, J. Grant, personal communication). Thus, vole populations in the Mission Valley may be relatively uncorrelated for much of the cycle but may be correlated during extreme highs and lows.

Disparity between $\hat{\lambda}$ and $\hat{C}_{max}$

Detailed examination of Figures 1 and 2 and Tables A1 and A2 will reveal that often $\hat{\lambda} > 1.0$ when $\hat{C}_{max} < 1.0$. In fact, $\hat{\lambda}$ exceeded $\hat{C}_{max}$ in many years. Two explanations may account for this disparity. First, immigration does not affect C but does increase λ; thus if large immigration rates support a population, then we would expect λ to far exceed C. Second, β may have been underestimated, which would lead to underestimation of C but not of λ, because $\hat{\beta}$ was not used in the estimation of λ.

Occasionally, $\hat{\lambda}$ was demonstrably large due to immigration. For instance,

119

between August and September of 2003 on grid SG, estimated abundance of meadow voles in ungrazed habitat increased from 1.0 to 14.6 individuals (Figure 1) resulting in $\hat{\lambda}$ of 14.6. No juveniles were captured during September 2003 thus the observed increase was due entirely to immigration (note that capture probabilities were allowed to vary between trapping sessions and were not a cause of the increase in $\hat{\lambda}$). In September 2004 on grid DK, the area on the ungrazed side of the fence received a grazing treatment due to management concerns regarding invasive weeds. An electric fence provided a buffer of 50 to 100 m between the trapping grid and livestock. Estimated abundance was 76 for montane voles and 0 for meadow voles in August 2004. Grazing occurred immediately following the August trapping session, and in September 2004, estimated abundance was 107 for montane voles and 9 for meadow voles (Fig. 1). No voles caught in September were juveniles, and closed capture probabilities were allowed to vary by trapping session, again making immigration the most likely cause for the population increase.

However immigration events such as these do not always occur and thus did not always cause the disparity between $\hat{\lambda}$ and $\hat{C}_{max}$. Large differences between $\hat{\lambda}$ and $\hat{C}$ also occurred in the spring when β is highest for voles in the study area. Potential underestimation of β_{max} would certainly bias the estimation of C_{max}. I discuss this issue relative to source-sink classification below.

Spatial Structure of Vole Populations

The manner in which local populations interact with each other and with the habitat in which they are located can have profound effects for a multi-site population. For instance, if local populations are weakly coupled by dispersal, then we can expect populations in sink habitat to be ephemeral. However, if local populations are coupled by

120

higher rates of dispersal, sources can maintain sinks perpetually. In this study, meadow voles appeared to exhibit the former type of dynamic and montane voles the latter. Before any conclusions regarding source-sink dynamics can be made though, the alternative hypotheses of balanced dispersal, unbalanced dispersal, reciprocating dispersal, sink-sink, and source-source dynamics must be addressed.

Evidence suggests that livestock grazing imposed source-sink structure on populations of montane and meadow voles. Dispersal generally flowed from ungrazed to grazed habitat (Table 2), and $\hat{C}_{max}$ was higher in ungrazed habitat than in paired grazed habitat for 11 of the 12 grid/year combinations for montane voles (Table A1) and 8 of the 12 combinations for meadow voles (Table A2). The balanced dispersal model predicts equal numbers of individuals dispersing between habitats while the unbalanced dispersal model predicts more individuals dispersing from grazed to ungrazed habitat than vice versa. In two cases for montane voles, dispersal probability from ungrazed to grazed habitat was greater than 0 and nearly equal to dispersal probability from grazed to ungrazed habitat (Table 2), but, because abundances were generally higher in ungrazed than in grazed habitat, equal probability of dispersal between habitats translates to more individuals dispersing from ungrazed to grazed habitat than vice versa. Thus, for both species, overall dispersal patterns did not conform to the balanced or unbalanced dispersal models. However, the three competing theories of reciprocating dispersal, sink-sink, and source-source dynamics need further comparison with source-sink dynamics.

Both balanced dispersal and source sink dynamics have occurred over time in the same population of rodents (Morris and Diffendorfer 2004, Tattersall et al. 2004), potentially leading to patterns of reciprocating dispersal (Morris et al. 2004). The theory

121

of reciprocating dispersal predicts that dispersal will flow from sub-optimal to optimal habitat when abundance is low in optimal habitat and that the opposite pattern will occur when abundance is high in optimal habitat. Although the overall net flow of dispersal was generally from ungrazed to grazed habitat, dispersal events did occur in the opposite direction for two populations of montane vole and one population of meadow vole (Table 3). In all three cases (grid SG year 2004 for montane vole and meadow vole, grid DK year 2003 for montane vole), abundance was higher in ungrazed habitat than in grazed habitat, which suggests that dispersers were not responding to abundance patterns in the two habitats. However, for the grid SG in year 2004, abundances of the two species were much lower than they had been in previous years; thus dispersal back to ungrazed habitat may have been due to the availability of territories there. Nevertheless, if reciprocating dispersal was a consistent pattern in the study populations, I would have expected to see dispersal from grazed to ungrazed areas whenever abundance was declining or low. Four grid/year combinations were sampled when they were in declining or low phases for montane voles, and in only one was dispersal observed from grazed to ungrazed habitat. Similarly in five cases where meadow vole populations were in declining or low phases and populations of meadow voles concurrently existed in grazed habitat, dispersal from grazed to ungrazed habitat occurred only once. Additionally, differences in directional dispersal through a cycle revealed no patterns. These observations suggest that reciprocating dispersal is rare in the study system and that sink-sink, source-source, or source-sink dynamics is the dominant paradigm through cyclic changes in abundance.

Potentially, all areas sampled could be sinks, and unsampled source habitat could be driving system dynamics. Voles occur in five very broad types of habitat in the study

122

area: grazed grassland, ungrazed grassland, tilled cropland, fallow cropland, and wetland margins. Both tilled and fallow areas have less vegetative cover than ungrazed areas and are unlikely candidates for source habitat. Wetlands occur throughout the Mission Valley and may have represented source habitat, but these areas occupy an extremely small proportion of the valley. If these areas are sources and the rest of the habitats sinks, then very high rates of reproduction and emigration would be needed to maintain populations in all other habitats, which is unlikely given that many studies have been conducted on these species and not one has described wetlands as habitat of prime importance (e.g., Findley 1951, Murie 1971, Hodgson 1972, Douglass 1976, Birney et al. 1976, Grant et al. 1982, review in Getz 1985, Bowers et al. 1996, Getz et al. 2005). Thus, the possibility of sink-sink dynamics operating on a broad scale can be rejected.

Processes operating at hierarchies beneath the patch level may have caused sampled areas in ungrazed habitat to be sinks. Sampled areas were near fences, and perched raptors may have induced sink-like conditions in nearby ungrazed habitat (Wolff et al. 1999). Anecdotal observations of raptor activity suggest that raptors neither forage exclusively near fences nor forage at high enough activity and success rates to maintain sink-like conditions there.

A final possibility for sink-sink dynamics is that the study itself induced sink-like conditions in ungrazed areas (e.g., Clinchy et al. 2001). Possibly, the death of pregnant voles in traps drastically altered natural trajectories of local recruitment. If so, the proportion of young caught at time $i + 1$ should be negatively correlated with the proportion of adult females that expire in traps at time i. However, a simple linear regression indicated the opposite effect and was not statistically significant (slope

123

coefficient = 0.17, SE = 0.35, p = 0.63). Although handling effects remain a possibility for causing sink-like conditions in ungrazed areas, the likelihood seems low.

The most likely explanation for multiple values of $\hat{C}_{max} < 1$ in ungrazed habitat is the effect of off-sample-site emigration (E_{oss}) and potential mis-estimation of per capita reproduction (β). The estimates of apparent survival ($\hat{S}$) presented here are biased low in terms of true survival because individuals may leave the study area yet stay in the area of interest. Additionally, the weight criteria used to distinguish young from adults are conservative: any individual labeled a juvenile with these criteria is almost certainly a juvenile, but some juveniles may have been mis-labeled adults leading to underestimation of β.

A robust analysis of sources and sinks requires incorporation of uncertainty for estimates of E_{oss} and β (Fig. 4). For montane voles in ungrazed habitat, if β were 0.3, E_{oss} of adults and juveniles would have to be 0.11 for ungrazed habitat to be a source (Fig. 4). Rates of emigration exceeding 0.11 have been observed previously in *Microtus* species (Coffmann et al. 2001, Williams et al. 2002), which suggests that ungrazed habitat may act as a source for montane voles even at levels as low as 0.3 young per adult. If β were 0.3 in grazed habitat, E_{oss} of adults and juveniles would have to be 0.25 for grazed habitat to be a source (Fig. 4). An emigration rate of 0.25 is fairly high for voles (see review in Bowne and Bowers 2004), but note that if β were 0.5, E_{oss} would have to be 0.14 for grazed habitat to be a source. Thus the possibility of source-source dynamics remains plausible for montane voles.

The average value of $\hat{S}$ for meadow voles was similar to that for montane voles, which suggests that ungrazed habitat generally functions as a source, given realistic

124

values for E_{oss} and β (Fig. 4). The same is not true for meadow voles in grazed habitat. With $\beta = 0.5$, E_{oss} would have to be 0.25 for grazed habitat to be a source (Fig. 4). Even with β as high as 0.8, E_{oss} would have to be 0.14 for grazed habitat to be a source. Thus, grazed habitat likely functions as a sink for meadow voles, and the ephemeral occurrence of meadow vole populations in grazed areas (Fig. 1) suggests that immigrants from ungrazed habitat periodically recolonize grazed habitat.

One possible alternative remains for populations of montane voles: both habitats could be sources without displaying the properties of balanced, unbalanced, or reciprocating dispersal. The balanced and reciprocating dispersal models are based upon equilibrium dynamics, that is abundance is allowed to go to carrying capacity either across evolutionary time (the balanced dispersal model, McPeek and Holt 1992) or within a season (the reciprocating dispersal model, Morris et al. 1994). Disturbance dynamics operating over the course of weeks, rather than equilibrium dynamics operating over the course of months or years, may control vole populations in grazed areas. Between grazing rotations, grazed habitat becomes increasingly more suitable to voles. When cattle are allowed back on to grasslands, an abrupt change in vegetation structure occurs, preventing vole populations from reaching equilibrium. Montane vole populations in grazed habitat may become sources as vegetation recovers from bovine disturbance then revert to sink status when cattle return. Indeed, the analysis of $\hat{S}$ in relation to vegetation height-density suggests a strong effect of vegetation removal on $\hat{S}$ (Fig. 3). A similar graphical analysis suggests that $\hat{C}$ specific to primary period increases as vegetation height-density increases, reaching values near 0.9 as average Robel measurements near 10 (Fig. 5). The positive slope of $\hat{C}$ in response to vegetation height-density considered

125

along with emigration from the sample space and estimates of β that are biased low suggest that as vegetation height-density increases, populations of montane vole in grazed habitats may become sources. Therefore, populations of montane vole in grazed habitat may occasionally act as sources, occasionally as sinks, and land managers may be able to maintain grasslands as sources or sinks for voles solely by controlling conditions of vegetative cover.

Management Implications

Evidence presented here suggests that livestock grazing induces a source-sink structure in vole populations. Population fitness is greater in ungrazed than in grazed habitat (Fig. 2, Tables A1 and A2), and when patterns of emigration are considered (Table 3), ungrazed habitat appears to be a source while heavily-grazed habitat appears to be a sink. Although ungrazed habitat generally contains more voles than grazed habitat (Fig. 1), vegetative conditions there do not seem to affect vole abundance or apparent survival. This suggests that at some threshold level, vegetative conditions attract and maintain vole populations, but above the threshold, cover conditions do not strongly affect population dynamics. Conversely, vegetative cover within grazed habitat appears to influence apparent survival (Fig. 3) and therefore population fitness (Fig. 5), which suggests that land managers can induce source-sink conditions by increasing the density of cattle and thereby the intensity of grazing. Thus, livestock grazing may be a viable strategy if land managers wish to minimize the abundance of voles in certain areas.

However, land managers generally must consider multiple goals, and both livestock grazing and vole abundance may affect the ecosystem in multiple ways. For example, the reestablishment of native grasses may be more successful when vole

126

abundance is reduced, because voles can severely depredate grass seeds and shoots (Bard et al. 2004). Thus, land managers wishing to reestablish native grasslands may desire to graze livestock in areas surrounding tracts of ground where native grasses are to be reintroduced. One concern with this approach is that deer mice (*Peromyscus maniculatus*) are also granivores and may be unaffected by livestock grazing. A more troubling concern is the size of the area to be grazed. If land managers wish to reintroduce native grasses on a square, 100 ha tract, and a 200 m grazed strip surrounding the tract of reintroduction is sufficient to reduce vole abundance in the immediate area, then 80 hectares would have to be grazed. In this example, a total of 180 ha would be reduced to conditions of low vegetative cover, which would negatively affect biological processes such as production of ground-nesting birds (Fondell and Ball 2004). By a simple geometric relationship, the more rectangular the tract of native grass reestablishment becomes, the more area must be grazed to isolate it. Therefore if large areas are considered for reestablishment of native grasses, and livestock grazing is used to control vole populations, then production of ground-nesting birds would be impacted, and biodiversity would be reduced though both the reduction of vole populations (which would affect many predator populations) and through the homogenization of habitat at the landscape scale. In summary, the use of livestock grazing for specific management purposes such as native grass reestablishment can have strong negative effects on the environment and should be conducted with careful planning.

Voles strongly influence their surrounding habitat, potentially affecting local economies negatively through crop degradation and positively through enhancement of biodiversity. Livestock grazing can induce source-sink structure in vole populations and

127

thus may be an effective tool for managing vole populations. However, land managers generally need to consider multiple goals and, because voles affect the ecosystem in many ways, the reduction of vole abundance may aid the attainment of certain goals while detracting from others.

Table 1. List of statistics and parameters used. M refers to montane voles, P to meadow voles.

Statistic	Definition
n_U^*	Number of individuals of species U, $U \in \{M,P\}$, that were caught in a given primary period and a given habitat and that were later received a confirmed species identification
n_U^{est}	Number of individuals that were caught in a given primary period and a given habitat and that received a conditional assignment of species U but were never identified to true species.
$\hat{n}_U'$	Estimated number of individuals of species U that received conditional species assignments but were never identified to true species.
n^{unk}	Number of individuals that were caught in a given primary period and a given habitat and that never received a conditional species assignment nor a confirmed species identification.
$\hat{n}_U^*$	Estimated number of individuals of species U that were caught in a given primary period and a given habitat and were never identified to true species.
$\hat{N}_U$	Estimated overall abundance of species U in a given habitat during a given primary period.
S_U	Probability of survival for species U in a given habitat between two primary periods
ψ_U	Probability of dispersal in a given direction between habitats for species U.
π_U	Probability that an individual first captured in a given primary period and habitat is a member of species U.
δ_U	Probability that an individual of species U is correctly assigned to species U in a given primary period and habitat.
η_U	Probability that an individual of species U survives capture at period i in a given primary period and habitat to be released.
p_U	Probability of recapture for species U in given primary period and habitat.
p_U^*	Probability of capture for species U in a given primary period and habitat (conditioned on animals both initially captured and recaptured in the primary period of interest)
β_U	Per capita reproduction for species U in a given primary period and habitat
C	A measure combining reproduction, apparent survival, and emigration that is used to delineate sources and sinks.
C_{max}	The maximum measure of C from a given grid in a given year.
E_{oss}	Emigration from the sample space.

129

Table 2. Values of apparent survival ($\hat{S}$) (and bootstrapped standard errors) for females on all grids that received the treatment of livestock grazing. "Ung" denotes the half of the grid left idle for the duration of the study, "Grz" denotes the half of the grid that was grazed regularly. Values in parentheses with a * denote the number of releases upon which the estimate was based rather than the SE, and "n/a" indicates that no individual receiving that particular species assignment was caught in that particular habitat during that year.

Grid/Year	Montane vole		Meadow vole	
	Ung	Grz	Ung	Grz
CS 2002	0.572 (0.195)	0.477 (0.164)	0.701 (0.149)	0 (4*)
CS 2003	0.303 (0.289)	0 (1*)	0.243 (0.105)	n/a
CS 2004	0.802 (0.047)	0.548 (0.326)	0.111 (0.120)	n/a
DK 2002	0.569 (0.101)	0.600 (0.145)	0.822 (0.298)	0.108 (0.184)
DK 2003	0.849 (0.045)	0.761 (0.050)	0.821 (0.108)	0.974 (0.345)
DK 2004	0.861 (0.027)	0.698 (0.122)	0 (3*)	n/a
SG 2002	0.109 (0.040)	0 (1*)	0.947 (0.007)	n/a
SG 2003	0.843 (0.209)	0.678 (0.061)	0.695 (0.046)	0.337 (0.084)
SG 2004	0.614 (0.066)	0.628 (0.099)	0.722 (0.163)	0.207 (0.206)
ST 2002	1 (6*)	0 (3*)	0.411 (0.144)	1 (5*)
ST 2003	0.793 (0.056)	0.720 (0.083)	0.575 (0.049)	0.447 (0.122)
ST 2004	0.626 (0.101)	0.155 (0.152)	n/a	0.391 (0.210)

Table 4. Model selection results from linear regression of vegetation variables on species-specific abundance in ungrazed habitat. K is the number of parameters, grass = % grass cover, brgrnd = % bare ground, forb = % forb cover, species indicates that different main effects for montane and meadow voles were fit, and null is the intercept only model. ΔAIC_c is the difference in AIC_c units between the referenced model and the model with the lowest AIC_c.

Model	ΔAIC_c	K
null	0	2
grass	0.40	3
litter	0.42	3
litter * species	1.00	5
brgrnd	1.73	3
species	1.89	3
forb	2.37	3
grass + species	2.48	4
litter + species	2.51	4
robel	2.62	3
brgrnd + species	3.86	4
forb + species	4.52	4
robel + species	4.73	4
grass * species	5.13	5
brgrnd * species	7.00	5
forb * species	7.67	5
robel * species	7.96	5

132

Table 4. Model selection results from linear regression of vegetation variables on species-specific abundance in ungrazed habitat. K is the number of parameters, grass = % grass cover, brgrnd = % bare ground, forb = % forb cover, species indicates that different main effects for montane and meadow voles were fit, and null is the intercept only model. ΔAIC_c is the difference in AIC_c units between the referenced model and the model with the lowest AIC_c.

Model	ΔAIC_c	K
null	0	2
grass	0.40	3
litter	0.42	3
litter * species	1.00	5
brgrnd	1.73	3
species	1.89	3
forb	2.37	3
grass + species	2.48	4
litter + species	2.51	4
robel	2.62	3
brgrnd + species	3.86	4
forb + species	4.52	4
robel + species	4.73	4
grass * species	5.13	5
brgrnd * species	7.00	5
forb * species	7.67	5
robel * species	7.96	5

132

Figure 1. Estimated abundance ($\hat{N}$) of montane voles (denoted "M") and meadow voles ("P") in ungrazed ("ung") and grazed ("grz") habitat on the four grids. Year and month are on the x-axis. A three-week interval separates sample periods within each year.

133
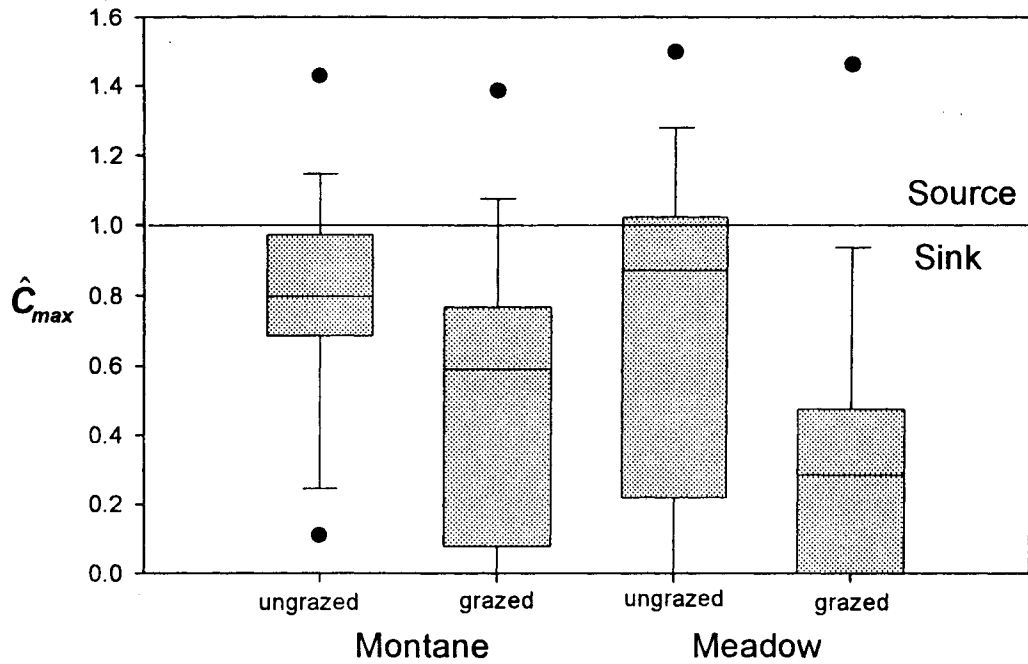
Figure 2. Maximum estimated values of C ("C$_{max}$") from each grid in each year (N = 12) for montane voles ("M") and meadow voles ("P") in ungrazed habitat ("ung"), and grazed habitat ("grz"). Lines within boxes mark medians, boundaries of the box mark 25th and 75th percentiles, whiskers mark 10th and 90th percentiles, and dots mark minima and maxima.

134
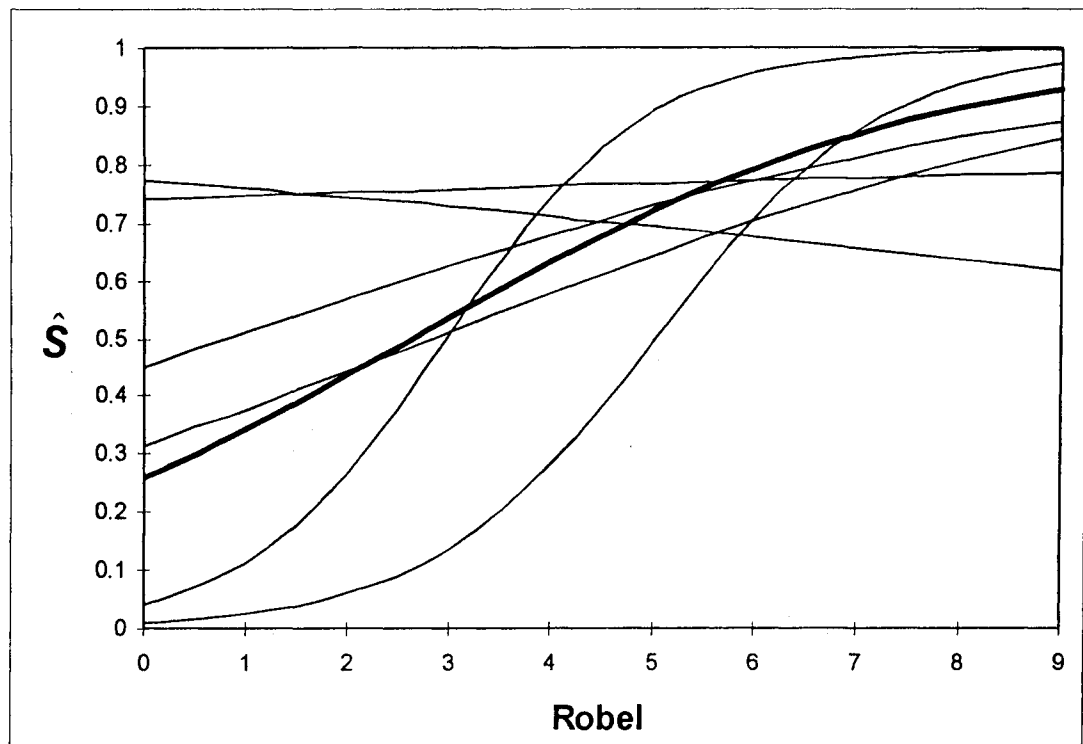
Figure 3. Values of apparent survival ($\hat{S}$) from models fit to average Robel

measurements in grazed habitat. The bold line is the mean value for the intercept and

slope back-transformed from within the logit expression, and the lighter lines are the

particular grid/year combinations from which the mean values are derived. Robel units

are 5 cm; thus the value 9 on the x-axis would correspond to a Robel reading 45 cm from

the ground.

135
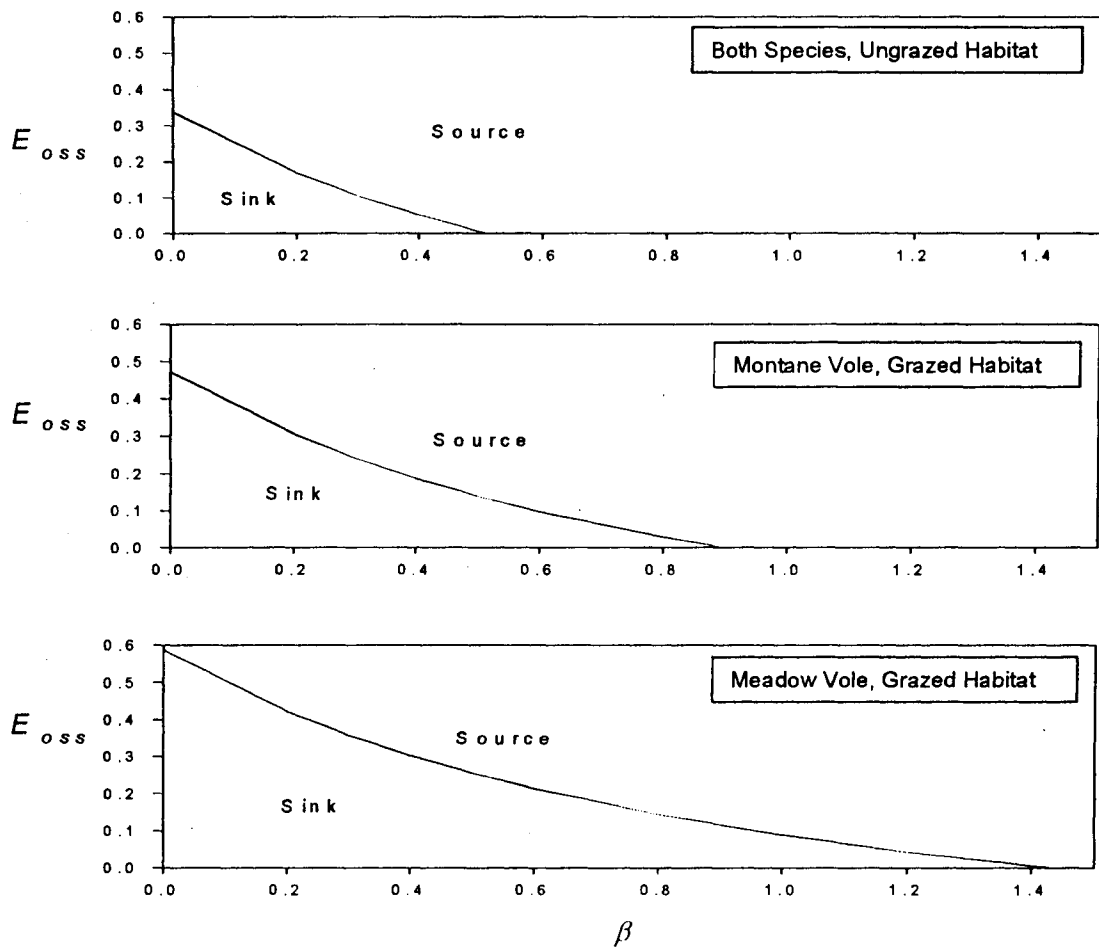
Figure 4. The effect of uncertainty in population estimates on source-sink designation for

the two species in the two habitats. The line represents values of per capita recruitment

(β) and emigration from the sample space (E_{oss}) needed to achieve a value of $C = 1.0$

given values of apparent survival ($\hat{S}$) averaged over the 4 grids and 3 years of the study.

Montane and meadow vole in ungrazed habitat had near identical values of average $\hat{S}$ and

thus are presented in the same panel. Any point on or above the line would indicate the

habitat is a source, any point below the line would indicate a sink. For instance, if β was

hypothesized to be 0.8 for meadow voles in grazed habitat and E_{oss} was hypothesized to

be 0.1, grazed habitat would be a sink given the average value of $\hat{S}$.

136

$\hat{C}$

1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0

0   2   4   6   8   10
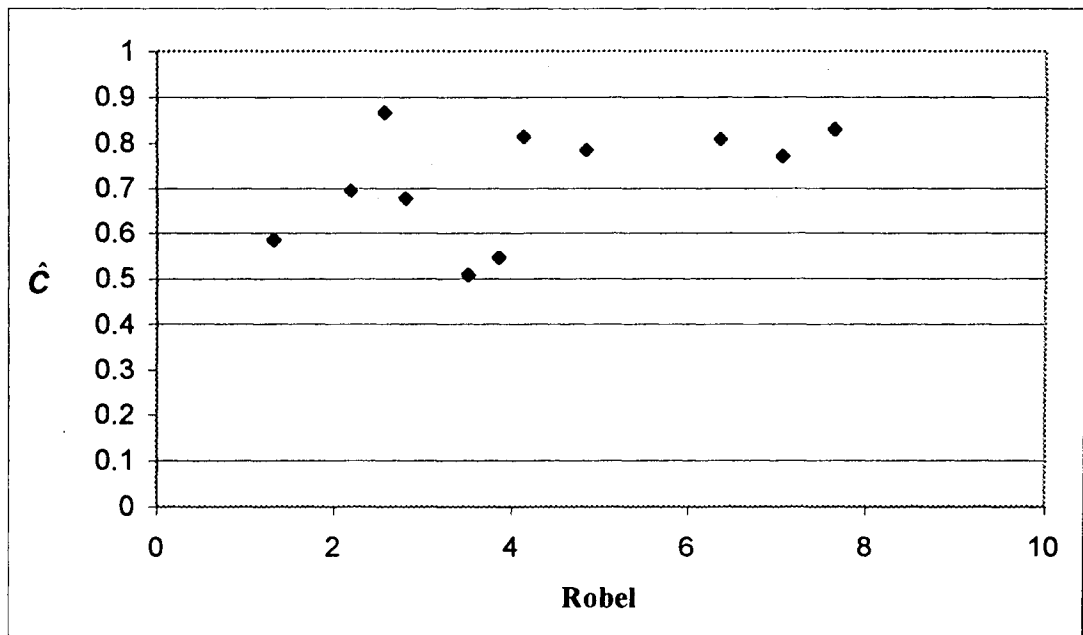
Robel

Figure 5. Scatterplot of time-specific values of $\hat{C}$ and vegetation height density ("Robel"). Measurements of $\hat{C}$ were taken from grids and years in which sufficient captures of montane voles enabled estimation of time-specific survival and are from the first three primary periods (May-June) when reproduction was highest.

137

Values of contributions for ungrazed habitat ($\hat{C}^{ung}_{max}$) and grazed habitat ($\hat{C}^{grz}_{max}$)

for each grid in each year.

Table A1. Montane vole.

Grid	Year	$\hat{C}^{ung}_{max}$	$\hat{C}^{grz}_{max}$
CS	2002	0.67	0.54
CS	2003	0.30	0.00
CS	2004	1.02	0.55
DK	2002	0.75	0.70
DK	2003	0.90	0.77
DK	2004	0.94	0.76
SG	2002	0.11	0.00
SG	2003	0.84	0.94
SG	2004	0.70	0.63
ST	2002	1.00	0.00
ST	2003	1.43	1.39
ST	2004	0.72	0.16

Table A2. Meadow vole.

Grid	Year	$\hat{C}^{ung}_{max}$	$\hat{C}^{grz}_{max}$
CS	2002	0.84	0.00
CS	2003	0.24	0.00
CS	2004	0.20	0.00
DK	2002	1.18	0.18
DK	2003	0.90	1.46
DK	2004	0.00	0.00
SG	2002	1.01	0.00
SG	2003	0.95	0.47
SG	2004	1.50	0.48
ST	2002	1.04	0.45
ST	2003	0.62	0.71
ST	2004	0.00	0.39

138

Appendix B Chapter 4

Parameter estimates taking uncertain species identification into account.

S is the probability of apparent survival, ψ is the probability of dispersal, p is the probability of recapture, π is the probability of an animal being a montane vole, δ is the probability of correct classification, and η is the probability of release. Est. is the point estimate for the parameter of interest, and SE is the standard error for the point estimate. G-U designates dispersal from grazed to ungrazed habitat, "sum" designates summer, n/a indicates that no voles were caught on which to base an estimate, and * in the SE column indicates that no estimate of standard error was available due either to paucity of data or an estimate of 0 or 1. Estimates of η in 2004 were not fit by season because all trapping in spring 2004 took place during daytime hours, resulting in few mortalities.

Table B1. Grid CS.

Parm.	Species	Habitat	2002 Est.	2002 SE	2003 Est.	2003 SE	2004 Est.	2004 SE
S	montane	ungrazed	0.572	0.195	0.303	0.289	0.802	0.048
S	montane	grazed	0.477	0.164	0	*	0.548	0.326
S	meadow	ungrazed	0.701	0.149	0.243	0.105	0.111	0.200
S	meadow	grazed	0.251	0.217	n/a	*	n/a	*
ψ	montane	u-g	0.070	0.172		*	0	*
ψ	montane	g-u	0	*	0	*	0	*
ψ	meadow	u-g	0	*	0	*	0	*
ψ	meadow	g-u	0	*	n/a	*	n/a	*
p	pooled	pooled	0.622	0.169	0.629	0.139	0.852	0.059
π		ungrazed	0.336	0.088	0.299	0.133	0.814	0.073
π		grazed	0.972	0.099	n/a	*	1	*
δ	montane	pooled	0.936	0.074	0.874	0.090	0.800	0.045
δ	meadow	pooled	0.920	0.072	0.934	0.073	0.921	0.075
η spring	montane	pooled	0.728	0.141	1	*		
η sum	montane	pooled	0.972	0.030	1	*	0.984	0.011
η spring	meadow	pooled	0.704	0.141	1	*		
η sum	meadow	pooled	0.964	0.040	1	*	0.926	0.085

139

Table B2. Grid DK.

Param.	Species	Habitat	2002		2003		2004	
			Est.	SE	Est.	SE	Est.	SE
S	montane	ungrazed	0.569	0.101	0.849	0.045	0.861	0.027
S	montane	grazed	0.600	0.145	0.761	0.050	0.698	0.122
S	meadow	ungrazed	0.822	0.298	0.821	0.108	0	*
S	meadow	grazed	0.108	0.184	0.974	0.345	n/a	*
ψ	montane	u-g	0	*	0.016	0.007	0.020	0.013
ψ	montane	g-u	0	*	0.016	0.016	0	*
ψ	meadow	u-g	0.223	0.444	0	*	0	*
ψ	meadow	g-u	0	*	0	*	n/a	*
p	pooled	pooled	0.630	0.098	0.575	0.028	0.710	0.048
π		ungrazed	0.928	0.052	0.821	0.038	0.923	0.025
π		grazed	0.832	0.153	0.965	0.049	1	*
δ	montane	pooled	0.967	0.019	0.985	0.010	0.979	0.016
δ	meadow	pooled	0.682	0.094	0.799	0.113	0.675	0.109
η spring	montane	pooled	0.783	0.078	0.894	0.022		
η sum	montane	pooled	0.941	0.030	0.969	0.007	0.929	0.016
η spring	meadow	pooled	0.806	0.160	0.855	0.069		
η sum	meadow	pooled	1	*	0.919	0.062	0.884	0.148

140

Table B3. Grid SG.

Parameter	Species	Habitat	2002		2003		2004	
			Est.	SE	Est.	SE	Est.	SE
S	montane	ungrazed	0.109	0.040	0.844	0.209	0.615	0.067
S	montane	grazed	0	*	0.678	0.061	0.628	0.099
S	meadow	ungrazed	0.947	0.007	0.695	0.046	0.722	0.163
S	meadow	grazed	0	n/a	0.337	0.084	0.207	0.206
ψ	montane	u-g	0	*	0.109	0.325	0.068	0.052
ψ	montane	g-u	0	*	0	*	0	*
ψ	meadow	u-g	0	*	0.036	0.016	0	*
ψ	meadow	g-u	0	*	0	*	1	*
p	pooled	pooled	0.297	0.116	0.566	0.051	0.889	0.063
π		ungrazed	0.206	0.077	0.067	0.029	0.830	0.067
π		grazed	0.860	0.024	0.745	0.067	0.686	0.113
δ	montane	pooled	0.943	0.008	0.939	0.084	0.962	0.061
δ	meadow	pooled	0.926	0.013	0.943	0.008	0.929	0.035
η spring	montane	pooled	[a]	[a]	0.875	0.068		
η sum	montane	pooled	0.977	0.003	0.966	0.031	0.962	0.024
η spring	meadow	pooled	[a]	[a]	0.941	0.028		
η sum	meadow	pooled	0.942	0.016	0.991	0.008	0.831	0.092
η [b]	meadow	ungrazed			0.562	0.101		

[a] Grid SG was not trapped in spring 2002.
[b] During primary period 4 2003, extreme temerature resulted in a high number of mortalities by 10 AM..

141

Table B4. Grid ST.

Parameter	Species	Habitat	2002		2003		2004	
			Est.	SE	Est.	SE	Est.	SE
S	montane	ungrazed	1	*	0.794	0.056	0.626	0.101
S	montane	grazed	0	*	0.720	0.083	0.155	0.152
S	meadow	ungrazed	0.411	0.144	0.575	0.049	n/a	*
S	meadow	grazed	1.000	*	0.447	0.122	0.391	0.210
ψ	montane	u-g	0	*	0	*	0	*
ψ	montane	g-u	0	*	0	*	0	*
ψ	meadow	u-g	0	*	0.045	0.050	n/a	*
ψ	meadow	g-u	0	*	0	*	0	*
p	pooled	pooled	0.690	0.071	0.640	0.054	0.900	0.078
π		ungrazed	0.278	0.096	0.515	0.060	1	*
π		grazed	0.544	0.128	0.484	0.096	0.815	0.110
δ	montane	pooled	0.902	0.075	0.901	0.051	0.940	0.060
δ	meadow	pooled	0.883	0.062	0.841	0.101	0.857	0.076
η spring	montane	pooled	[a]	[a]	0.945	0.023		
η sum	montane	pooled	0.959	0.119	0.992	0.008	0.976	0.033
η spring	meadow	pooled	[a]	[a]	0.967	0.040		
η sum	meadow	pooled	0.979	0.029	0.940	0.040	1	*
η [b]	meadow	grazed			0.241	0.200		

[a] Grid ST was not trapped in spring 2002.
[b] During primary period 4 2003, a low-lying area of the grid was flooded at during the night resulting in the deaths of a number of meadow voles that had already been caught in traps.

142

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144

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