ABSTRACT OF DISSERTATION

ECOLOGICAL RESPONSES BY MEXICAN SPOTTED OWLS

TO ENVIRONMENTAL VARIATION IN THE

SACRAMENTO MOUNTAINS, NEW MEXICO

Understanding the influence of environmental variation on population processes is a fundamental requisite for devising strategies that conserve species. A common tactic for conserving raptor populations is to maintain or manipulate habitat conditions that maintain or increase availability of prey species. A primary purpose of this investigation was to evaluate the hypothesis that Mexican spotted owls (*Strix occidentalis lucida*) could be conserved by manipulating microhabitat conditions that increased abundance of one or more common prey species. I evaluated this hypothesis by (1) determining which common prey were preferred by this owl, (2) which prey species were most likely to influence the owl's reproduction, and by assessing (3) which prey species were most likely to increase in abundance following microhabitat manipulation. In addition to prey availability, I also examined the influence of two other likely sources of environmental variation, weather and macrohabitat condition, on spotted owl reproduction and common prey abundance. The investigation focused on one population of Mexican spotted owls over a six-year period (1991–1996) in the Sacramento Mountains, New Mexico; an area where vegetation communities have been modified extensively over the past 100 years.

Under current landscape conditions, I found that these Mexican spotted owls consumed a variety of prey species during the breeding season. However, five murid rodents were most common. These included the deer mouse (*Peromyscus maniculatus*), brush mouse (*P. boylii*), Mexican vole (*Microtus mexicanus*), long-tailed vole (*M. longicaudus*), and Mexican woodrat (*Neotoma mexicana*). Depending on the year of study, the five species accounted for 53–77 % of frequency of all items recovered from samples of regurgitated pellets and 41–66 % of biomass consumed by these spotted owls. Mexican woodrats were preferred among the five prey species. Absolute functional responses to available numbers of woodrats varied in form (a quadratic function) compared to responses to mouse (a linear function) and vole (an increasing but asymptotic function) abundance.

Total available biomass (kg) of mice and voles provided the strongest correlation ($r = 0.78$, $P = 0.07$, $n = 6$ yrs) with reproductive output (number of young found per pair) of Mexican spotted owls among a suite of covariates that included measures of weather, macrohabitat quantity, and available prey biomass over the six annual periods. There was little evidence that selected weather variables and macrohabitat quantities were associated with the owl's reproductive output (all $r < 0.50$, $P > 0.39$). Models of factors associated with reproductive potential (number of young produced in a given owl territory relative to maximum number possible during all years the territory was sampled) indicated that precipitation during the nesting period (March–May) played a greater relative role (relative importance based on a weighted Akaike criterion [RI] = 0.733) in explaining a limited amount of variation (R^2 of all models $\leq 23\%$) in the owl's reproduction among

territories. Weaker evidence suggested that the owl's reproductive potential varied inversely among territories with warmer temperatures during late fall–winter (RI = 0.447) periods or colder temperatures during the early nesting period (RI = 0.335), and varied positively with available biomass of mice and voles (RI = 0.331). In the current landscape, available biomass of Mexican woodrats, the preferred prey, was not correlated with the owl's annual reproductive output nor its reproductive potential.

Empirical models of factors that influence availability of these five common prey species indicated that the easiest species to influence through microhabitat manipulation would be the Mexican vole, followed by the long-tailed vole, Mexican woodrat, deer mouse, and lastly the brush mouse. The model results indicated that abundance (g/ha) of the two vole species could be influenced most readily by manipulating grass-forb height, whereas abundance of Mexican woodrats might be influenced by promoting shrub diversity and increasing large (≥30-cm diameter) log cover. Increase of the two mouse species was considered more difficult because of their association with seed or mast crops, which were influenced by uncontrollable variables like previous amounts of precipitation, or their association with microhabitat variables like rock cover.

Details regarding historical and current conditions in the study area and comparisons between a mixed-conifer, late-seral plot and a mid-seral plot indicated that microhabitat variables associated with Mexican woodrat abundance and the amount of woodrat biomass available to Mexican spotted owls likely declined with past timber harvest. Consumption of woodrats by spotted owls in the Sacramento Mountains was the lowest among reported studies of spotted owl feeding habits. When examined across

eight different populations of spotted owls, consumption of woodrat biomass (%) was found to be inversely related to temporal variability in the owl's reproductive output (R^2 = 0.66, 95% CI [β_1] = −0.941 to −0.163).

I therefore proposed that future management of habitat condition in the Sacramento Mountains should strive to reduce temporal variation in Mexican spotted owl reproduction by increasing abundance of Mexican woodrats, which may be possible through experimental manipulations of mid-seral mixed-conifer stands. The immediate objective of these manipulations would be to enhance key microhabitat features required by Mexican woodrats such as shrub evenness and den sites or foraging cover. These manipulations appear to be congruent with current demands to thin overstocked, mixed-conifer stands in the study area. By conducting these manipulations as experiments and monitoring the associated responses by Mexican woodrats and Mexican spotted owls, a more comprehensive understanding of effects of environmental variation on this predator-prey system can be gained.

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The seed of every investigation is a question to be answered. Its germination requires a particular environment and its nurture requires funding. The initial idea of conducting an investigation of environmental factors that influence Mexican spotted owls in the Sacramento Mountains, New Mexico, emanated from a meeting with Mr. Keith Fletcher (Southwestern Region, USDA Forest Service; FS) in February1990. Keith was instrumental in securing the initial funding for the study. Drs. Kieth Severson (now retired) and Bill Block (Rocky Mountain Research Station, USDA Forest Service; RMRS) were responsible for administering this research through RMRS and they helped to shape the design for a pilot study in 1991. During subsequent years Bill Block took the

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CHAPTER 1

INTRODUCTION

Conservation of focal species requires an understanding of how environmental variability affects population processes. A population will eventually decline to extinction if an adequate number of its members do not acquire sufficient resources to survive and reproduce. Typically, these resources are not distributed equally in space and time. In addition, environmental variation can alter life requisites of individuals within a population. Predictions about the capability of a landscape to support a particular species in the face of environmental variability are therefore greatly enhanced by functions which link demographic processes with resource availability.

Food is a key resource. There are several reasons why an emphasis on food would provide a logical focus for studying individual and population-level responses to environmental variability. First, food is a fundamental requisite for all animals because it provides the chemical energy, nutrients, and some to most of the water needed for survival, growth, and reproduction. Second, an animal's energetic and nutritional requirements, and hence the amount and types of food required, can vary with environmental conditions. Third, the availability of food for most organisms can vary considerably over space and time. Fourth, variability in food availability can stimulate behavioral and physiological responses in individuals that can ultimately result in changes

in a species' distribution or abundance (e.g., see Grant and Grant 1989). Accordingly, food is both a proximal cue for selecting habitat and an ultimate factor that influences individual fitness and population productivity (Lack 1946, Hildén 1965, White 1978).

Direct and indirect evidence supports the notion that food availability affects individuals and populations in the wild. Food for a variety of birds and mammals has been experimentally supplemented in natural settings. Many of these experiments have demonstrated short term effects on movements or demography (Boutin 1990). The influence of food is especially notable in raptor populations where distribution among habitats, density, fecundity, and movements are often highly correlated with food supply (Lack 1946, Newton 1979). Additional evidence can be seen in behaviors adapted by many organisms to deal with stochastic food supplies. These include caching or hoarding (Vander Wall 1990), specialized foraging (Stephens and Krebs 1986, Morrison et al. 1990), migration (Gauthreaux 1982, Terrill 1990), and hibernation or torpor (Lyman et al. 1982).

The relevance of food as a key factor affecting populations has not been ignored in conservation planning. Two recent strategies, one for conserving northern goshawks (*Accipiter gentilis*) and another for conserving Mexican spotted owls (*Strix occidentalis lucida*) in the southwestern United States are germane examples. Guidelines in both plans recommend conserving populations of the focal raptor by maintaining and restoring conditions within and among vegetation communities in a manner that will enhance the availability of the predator's prey on a landscape (Reynolds et al. 1992, USDI 1995). Conservation plans like these are based on a variety of ecological assumptions and are

best considered as working hypotheses (Murphy and Noon 1991). For example, there are two general assumptions inherent to the strategy indicated above for the northern goshawk and Mexican spotted owl; (1) prey abundance and availability can be enhanced by manipulating habitat features, and (2) demographic conditions of focal predator populations will be improved by the increased availability of prey. Empirical evaluation of these assumptions will not only lead to more reliable conservation strategies but improve our understanding of how predator populations respond to environmental variability.

In this study, I quantify two ecological responses by the Mexican spotted owl to environmental variability. The sources of environmental variation examined here include spatial and temporal variation in the abundance of this owl's common prey and variation in the owl's physical environment. I focus specifically on this owl's functional and numerical responses (Solomon 1949). In addition, I model the influence of several environmental factors on abundance of the owl's common prey.

The Mexican spotted owl is a threatened species and the focus of land management in the southwestern United States (USDI 1993; 1995). The findings from this study will provide information for conserving this owl and its environment.

The Predator

Spotted owls are medium-sized (450–700 g), nocturnal birds of prey. There are three subspecies of this owl. Northern spotted owls (*S. o. caurina*) occur in the near-coastal forests of the Pacific Northwest, ranging from northern California to southern British Columbia (Fig 1.1). Northern spotted owls require large contiguous tracts (~800–1,500 ha) of late seral coniferous forest to survive and reproduce. Loss and

fragmentation of this habitat through timber harvesting is considered a primary cause for the subspecies' documented decline (Bart 1995, Raphael et al. 1996, Meyer et al. 1998, but see also Franklin et al. 2000). The California spotted owl (*S. o. occidentalis*) ranges from north-central California through the Sierra Nevada Mountains into the mountain archipelago of southern California and into Baja California, Mexico (Fig. 1.1). In the northern sections of its range, California spotted owls also use large tracts of late seral conifer forest, whereas populations occurring further south also persist in areas dominated by oak woodlands (Verner et al. 1992). Mexican spotted owls occur in the forested mountains and canyons of the southwestern United States and portions of Mexico (Fig. 1.1; Ward et al. 1995). This subspecies appears to persist in environments with relatively more habitat heterogeneity and isolation compared to areas used by the other two subspecies (Keitt et al. 1995, Rinkevich et al. 1995). Additional information regarding the ecology of all three subspecies is reported by Gutiérrez et al. (1995) and a detailed treatise on the Mexican spotted owl can be found in USDI (1995). This study focuses on one population of Mexican spotted owls occurring in south-central New Mexico (Fig. 1.1).

The Prey

Spotted owls consume primarily small to medium-sized (10–300 g), nocturnal rodents (Gutiérrez et al. 1995). Although diet descriptions vary slightly with geographic region, spotted owls tend to consume greater amounts of medium-sized rodents like northern flying squirrels (*Glaucomys sabrinus*) and woodrats (*Neotoma* spp.) throughout most of their range (Thomas et al. 1990, Carey et al. 1992, Verner et al. 1992, Ward and Block 1995, White 1996, Ward et al. 1998, Smith et al. 1999, Forsman et al. 2001). One

exception appears to be Mexican spotted owls occurring in central and southern portions of their range. In these locations, medium-sized prey are consumed less than in other locations and smaller rodents like white-footed mice (*Peromyscus* spp.) or voles (*Microtus* spp.) are consumed in greater amounts (Ward and Block 1995). In the majority of cases it is unclear whether these food habits reflect preference or availability of prey.

Prey availability is considered a key influence on spotted owl behavior and demography. Habitat use by northern spotted owls has been positively associated with the distribution and abundance of flying squirrels or woodrats (Carey et al. 1992, Zabel et al. 1995, Ward et al. 1998). Reproductive success in the northern and California spotted owl also has been linked to the proportion of larger prey in the owls' diet (Thrailkill and Bias 1989, White 1996, Smith et al. 1999). However, reproductive success in Mexican spotted owls is believed to be more associated with the consumption of a variety of prey, including small species like mice and voles (Ward and Block 1995, Seamans and Gutiérrez 1999).

The Environment

This study was conducted in the Sacramento Mountains of south-central New Mexico, at the eastern edge of the Basin and Range physiographic province. The investigation was conducted on public land administered by the Sacramento Ranger District, Lincoln National Forest, USDA Forest Service (Fig. 1.2).

The Sacramento Mountains form a westerly escarpment that ascends precipitously from the Tularosa Basin at 1300 m to a maximum of 2930 m. Easterly slopes descend gradually to the Pecos River. Common soils are derived from San Andres limestone or

Yeso sandstone and include Cryoborolls (generally found from 2620 m to 2865 m in elevation), Argiborolls (2195 m to 2590 m), Ustorthents (2070 m to 2285 m), and Argiustolls (2010 m to 2135 m) (Ashford and Stury 1977).

Climate in the Sacramento Mountains is influenced by regional weather fronts and local, topographically induced conditions. Winter precipitation and cold temperatures are a function of polar air masses (Ashford and Stury 1977). In contrast, summer precipitation occurs primarily when low pressure systems draw moist air from the Gulf of Mexico southeasterly across arid surfaces and the warmed air condenses upon contact with cooler air situated above the mountains (commonly referred to as summer monsoons).

Locally, precipitation increases and temperatures decrease with elevation. For example, prior to the study period (1967–72; 1980–1990), mean annual precipitation ranged from 32 cm in Alamogordo (1326 m in elevation) to 75 cm in Cloudcroft (2652 m) while the temperature lapse over the same gradient was −0.83 °C per 100-m gain in altitude (Cooperative Weather Station Data, National Oceanic and Atmospheric Administration). Local weather also varies substantially among years and seasonally (Fig. 1.3). During the 17 years preceding this study, annual total precipitation at Cloudcroft ranged from 61 cm to 100 cm. Mean snow-depths during each measurable period (October–April) ranged from 0.1 cm to 20.8 cm and averaged 5.0 cm. Snow depths were below the seventeen-year average during 84 of 117 (72%) measurable months. Seasonally, 51% of the annual precipitation fell during July–September and coincided with warm temperatures (Fig. 1.3). Mean-monthly temperatures can vary as much as 18 °C within a year and daily temperatures can fluctuate an average of 11 °C to

15 °C. For example, during the 17 Junes, mean minimum and maximum temperatures ranged from 4.0 °C to 12.3 °C and from 20.3 °C to 26.4 °C, respectively. December mean minimum and maximum temperatures ranged from −11.4 °C to −1.2 °C and from 1.0 °C to 10.6 °C, respectively. Consequently, extremes in the physical environment may shift seasonally or annually but the coincidence of peak rainfall and warm summer temperatures usually induces productive growing conditions over much of this study area.

Extensive topographic relief, localized weather effects, and variable soil conditions within the Sacramento Mountains produce a broad ecological gradient typical of other southwestern ranges (Baily 1913). Using late-successional plant associations, the USDA Forest Service (1997) delineates 31 forest and woodland "habitat" types (*sensu* Daubenmire 1968) for this area. However, this study is restricted to three broad "habitats" (*sensu* Hall et al. 1997) that are likely to be used by Mexican spotted owls or their prey and include three forest or woodland types (Upper Montane Coniferous Forest, Lower Montane Coniferous Forest, and Coniferous Woodland; Moir 1993) and one grassland type (Montane; Dick-Peddie 1993).

Upper Montane Coniferous Forest occurs above 2280 m in elevation. This mixed-coniferous forest is usually dominated by Douglas-fir (*Psuedotsuga menziesii*) or white fir (*Abies concolor*). Well developed shrub and herbaceous layers are sometimes present with forbs more prevalent than grasses (Appendix 1.A). Lower Montane Coniferous Forest is found between 2070 m and 2590 m and is dominated by ponderosa pine (*Pinus ponderosa*). Shrubs are less prevalent and less diverse than in the Upper Montane Coniferous Forest while grasses tend to be more abundant. Conifer Woodlands occur below 2070 m and are dominated by two-needle pinyon pine (*P. edulis*) or juniper

(*Juniperus* spp.). Lower in elevation with a more open canopy, this community can include a well developed shrub and herb layer, with grasses more prevalent than forbs. Montane Grasslands are found in valley bottoms above 2130 m. These grasslands may also grade into "wet meadows" because of an association with drainage courses (Dick-Peddie 1993). This community is comprised of grasses and forbs and infrequently trees or shrubs encroaching from adjacent forests (Appendix 1.A).

Vegetation in the Sacramento Mountains has been substantially altered by anthropogenic disturbance during the past 100 years. Disturbances include extensive logging, grazing by domestic livestock, and agriculture (Kaufmann et al. 1998). Less than 5% of Upper Montane Conifer Forest stands are currently in a late seral condition whereas 10% to 26% are believed to have been in an "old-growth" (late seral) state in 1880 (Regan 1997). In addition, natural fire frequencies within the Upper Montane Conifer Forest (within-site means range 6–13 yrs) and Lower Montane Conifer Forest (within-site means range 4–8 yrs) have been suppressed and fire has been absent in many stands for 60–100 yrs (Brown et al. 2001). Outbreaks of some insects and pathogens have been amplified or introduced through past forestry practices and stand-replacing fires fueled by unnaturally dense forests have burned severely enough to convert forest types over large areas (Kaufmann et al. 1998). Further, many of the montane meadows were previously farmed and are undergoing succession similar to that observed in "old-fields." Thus, while the mosaic of plant communities in the Sacramento Mountains has been formed primarily by physical factors, the structure within these communities, and in some cases their spatial extent, have been altered dramatically by human-related activities within the past century.

Synopsis

Collectively, in the three chapters that follow, I evaluate the hypothesis that Mexican spotted owls can be conserved by manipulating habitat conditions of their primary prey. In Chapter 2, I examine the effects of microhabitat condition on abundance of the owl's common prey species relative to other potentially important factors. The hypothesis should be rejected if abundance of the owl's primary prey is not strongly influenced by habitat condition, particularly vegetation, that can be actively manipulated. In Chapter 3, I evaluate whether the owl is selective among common prey species and quantify the owl's functional response. The hypothesis would be most plausible if spotted owls exhibited a behavioral preference for a single prey species. In Chapter 3, I also examine the owl's reproductive output, a short-term numerical response to environmental variability. The hypothesis would be most plausible if prey species that are likely to respond to habitat manipulations and that are preferred by spotted owls, also stimulate the owl's reproduction. Lastly, in Chapter 4, I critique the hypothesis in light of the evidence provided in Chapters 2 and 3, and I discuss the implications of these findings with respect to the owl's conservation and future investigations.

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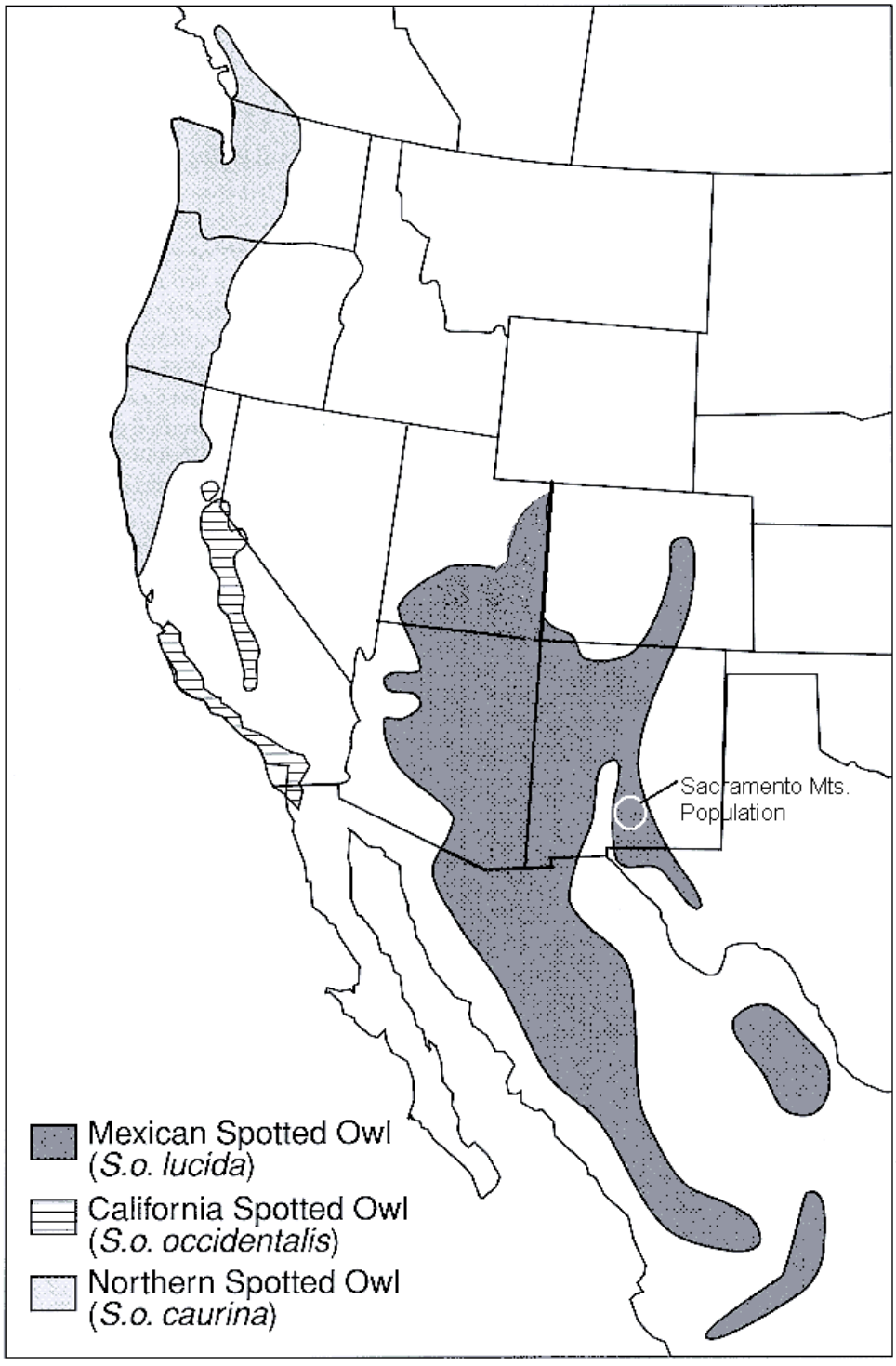

Figure 1.1. Range of three subspecies of spotted owl (*Strix occidentalis*) and location of the study population. Modified after USDI (1995).

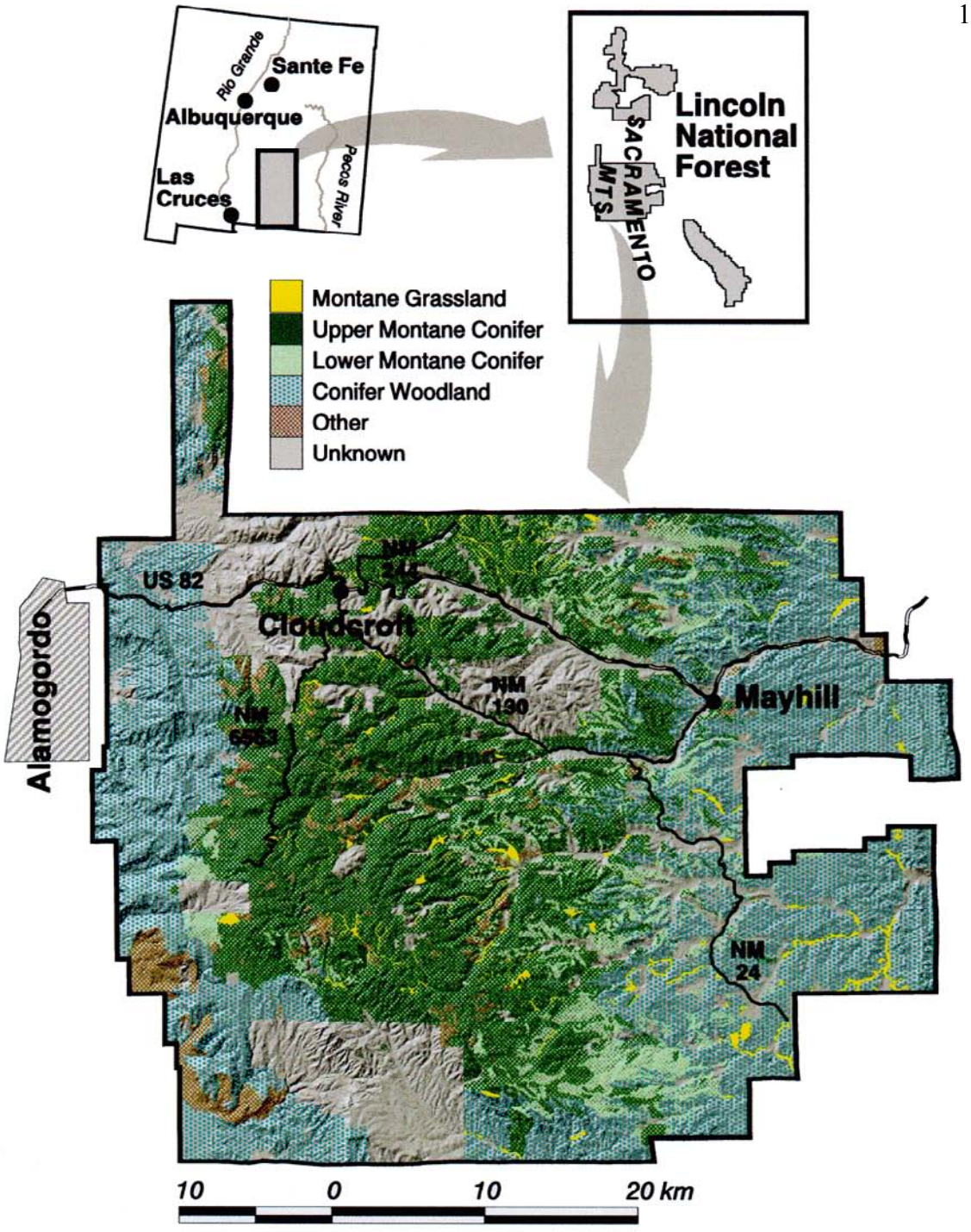

Figure 1.2. General vicinity and major vegetation communities in the southern Sacramento Mountains, New Mexico (based on Land Management Cover Types, USDA Forest Service, Lincoln National Forest, Alamogordo, New Mexico).

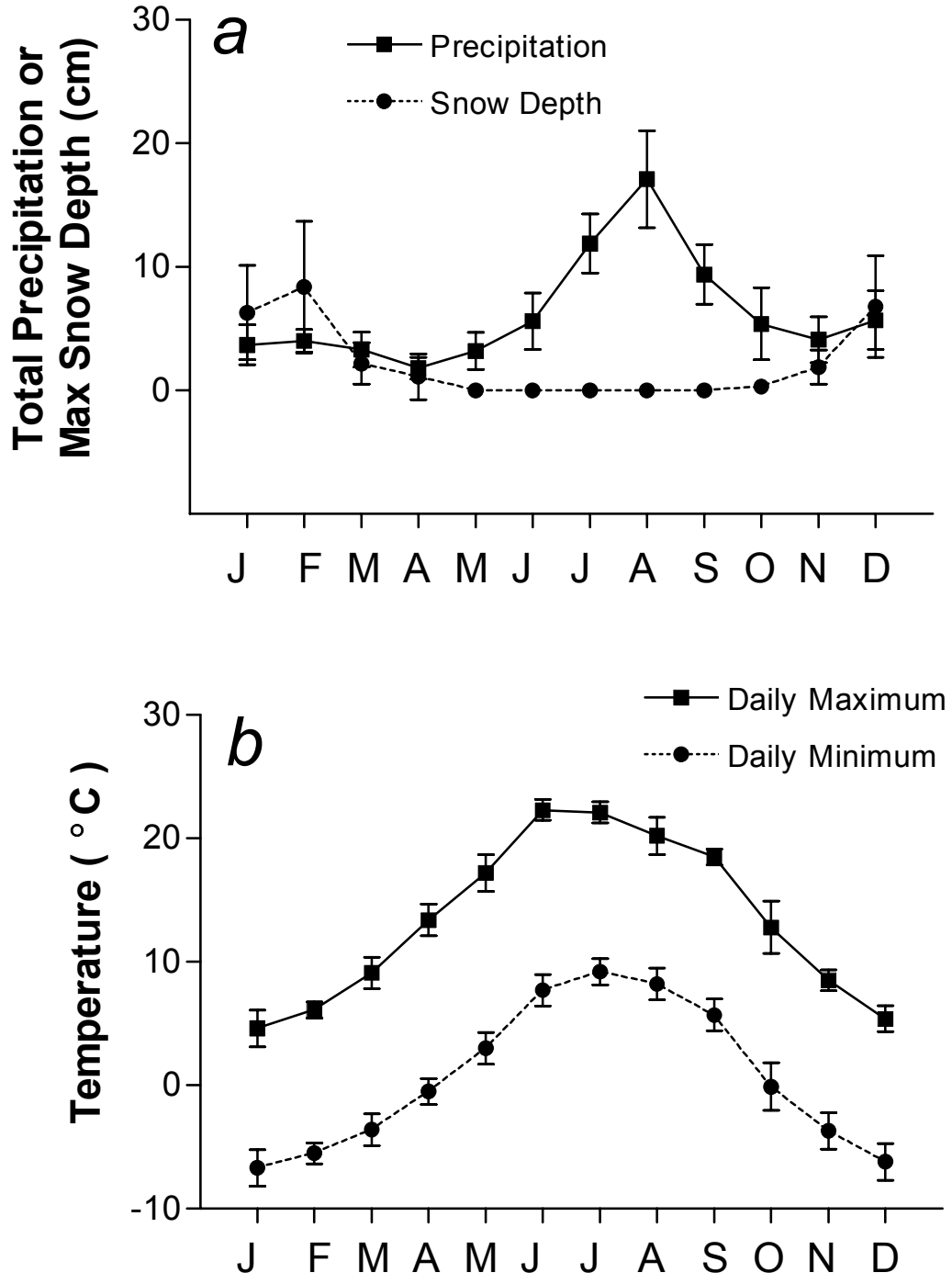

Figure 1.3. Temporal patterns of (*a*) rainfall, snow depth, and (*b*) temperature at Cloudcroft, New Mexico (1967–72; 1980–90). Vertical bars are 95% CI for mean-monthly estimates averaged among years. Data are from the Cloudcroft Cooperative Weather Station (National Oceanic and Atmospheric Administration)..

APPENDIX 1.A
Common Plants

Common plants of four major vegetation communities used by Mexican spotted owls or their prey in the Sacramento Mountains, New Mexico. Compiled from personal observation, USDA Forest Service records (Lincoln National Forest, *unpublished data*), and from literature. Asterisks denote non-native species.

Vegetation [a] Type	Common and Scientific Names of Plant Species by Growth Form [b]		
	trees	shrubs	herbs
Upper Montane Conifer Forest	Douglas-fir (*Pseudostuga menziesii*) white fir (*Abies concolor*) southwestern white pine (*Pinus strobiformis*) ponderosa pine (*P. ponderosa*) aspen (*Populus tremloides*) Gambel oak (*Quercus gambelii*) bigtooth maple (*Acer grandidentatum*) box elder (*A. negundo*)	rockspirea (*Holodiscus dumosus*) Gambel oak (*Quercus gambelii*) Oregongrape (*Mahonia repens*) boxleaf myrtle (*Paxistima mrysinites*) whortleleaf snowberry (*Symphoroicarpos oreophilus*) New Mexico locust (*Robinia neomexicana*) Rocky Mountain maple (*A. glabrum*) mountain ninebark (*physocarpus monogynus*) cliffbush (*Jamesia americana*)	Fendler meadowrue (*Thalictrum fendleri*) Richardson geranium (*Geranium richardsonii*) woodland strawberry (*Fragaria vesca*) Arizona peavine (*Lathyrus lanszwertii*) fringed brome (*Bromus ciliatus*) Canadian white violet (*Viola canadensis*) mutton grass (*Poa fendleriana*) starry false Solomon seal (*Maianthemum stellatus*)
Lower Montane Conifer Forest	ponderosa pine (*P. ponderosa*) twoneedle pinyon (*P. edulis*) Gambel oak (*Quercus gambelii*) alligator juniper (*Juniperus deppeana*)	true mountain mahogany (*Cercocarpus montanus*) skunkbush sumac (*Rhus trilobata*) small soapweed (*Yucca glauca*) Fendler ceanothus (*Ceanothus fendleri*)	hairy goldenaster (*Heterotheca villosa*) blue grama (*Bouteloua gracilis*) little bluestem (*Shizachyrium scoparium*) mountain muhly (*Muhlenbergia montana*) Lousiana sagewort (*Artemisia ludoviciana*)

APPENDIX 1.A. (Continued).

Vegetation [a] Type	Common and Scientific Names of Plant Species by Growth Form [b] trees	shrubs	herbs
Conifer Woodland	twoneedle pinyon (*P. edulis*) alligator juniper (*J. deppeana*) oneseed juniper (*J. monosperma*) Rocky Mountain juniper (*J. scopulorum*)	wavyleaf oak (*Quercus x pauciloba*) gray oak (*Quercus grisea*) skunkbush sumac((*Rhus trilobata*) true mountain mahogany (*C. montanus*) red barberry (*Mahonia haematocarpa*) bannana yucca (*Y. Bacata*) cliff fendlerbush (*Fendlera rupicola*)	blue grama (*B. gracilis*) sideoats grama (*B. curtipendula*) little bluestem (*S. scoparium*) big bluestem (*Andropogon gerardii*) bottlebrush squirrel tail (*Elymus elymoides*) common wolftail (*Lycurus pheloides*) manyflowered gromwell (*Lithospermum multiflorum*)
Montane Grassland			creeping bentgrass (*Agrostis stolonifera*) * fringed brome (*Bromus ciliatus*) Kentucky bluegrass (*Poa pratensis*) * orchardgrass (*Dachtylis glomerata*) * western yarrow (*Achillea millefolium var. lanulosa*) yellow thistle (*Cirsium pallidum*) Virginia strawberry (*Fragaria virginiana*)

APPENDIX 1.A. (Continued).

Vegetation [a] Type	Common and Scientific Names of Plant Species by Growth Form [b] trees	shrubs	herbs
Montane Grassland			purple geranium (*Geranium caespitosum*) orange sneezeweed (*Helenium hoopsei*) western blueflag (*Iris missouriensis*) clustered buttercup (*Ranunculus inamoenus*) cutleaf coneflower (*Rudbeckia lanciniata*) sheep sorrel (*Rumex acetosella*) * tuber starwort (*Stellaria jamesii*) common dandelion (*Taraxacum officianale*) * white clover (*Trifolium repens*) * Lousiana sagewort (*Artemesia ludoviciana*) black medic (*Medicago lupulina*) *

[a] Classification follows Moir (1993) and Dick-Peddie (1993).

[b] Nomenclature follows USDA Forest Service (1997); when not present in the latter source, names follow Ivey (1995).

CHAPTER 2

DISTRIBUTION AND ABUNDANCE OF FIVE MURID RODENTS : THE RELATIVE INFLUENCE OF HABITAT

Studies that describe distribution and abundance of small mammals are common in ecology. Like most organisms, small mammals vary in abundance over space and time. Ecological processes that generate these patterns are particularly germane to biological conservation. For example, assessment of certain environmental impacts, restoration of ecological systems, and preservation of endangered predators require an understanding of the factors that alter abundance and spatial distribution of small mammals (Kirkland 1990, Miller et al. 1990, Carey et al. 1992, Heske et al. 1994, Morrison et al. 1994, Baker et al. 1996, White and Garrot 1997).

Few ecologists would disagree that habitat selection is a key process that helps explain animal distribution and abundance. Accordingly, conservation strategies often rely on the "habitat" concept. This idea recognizes that distribution and abundance of a species is greatly influenced by the quantity, quality, and arrangement of resources used to fulfill life requisites of individuals, and that wild populations can therefore be sustained by conserving or manipulating these resources (Leopold 1933, Block and Brennan 1993, Hall et al. 1997, Noss et al. 1997). Although many small mammals are known to select habitat (M'Closkey and Fieldwick 1975, Thompson 1982a, Morris 1984,

Rosenzweig 1989, Vickery et al. 1989), a myriad of other influences can interact with resource use in complex ways to form the patterns of abundance ultimately observed at a given place and time (Andrewartha and Birch 1984, Wiens 1989, Rosenzweig 1991, Batzli 1992, Morris 1996, Hansson and Henttonen 1998). Efforts to develop reliable conservation strategies should therefore benefit from organism-habitat relationships that account for multiple ecological interactions.

Studies that relate effects of historical or biogeographic factors, habitat condition and selection, competition, predation, density dependence, or density-independent environmental factors to the structure of small mammal communities permeate the literature (e.g., see Morris et al. 1989 and references therein). Collectively, these investigations provide clues as to how various ecological processes interact to influence the distribution and abundance of a particular species. The following heuristic scenario illustrates how the distribution and abundance of small mammals may be shaped by multiple interactions.

Consider a hypothetical rodent searching for a place to settle. At the onset of its search, the character of the environment, including species with which this rodent will interact, and its own phenotype have long been cast through past biogeographic events and long-term population processes. A montane dwelling rodent in the southwestern United States, for instance, might encounter a suite of species remnant from once expansive forests reduced through vicariance events or species that arrived via expansive colonization (Findley 1969, Lomolino et al. 1989, Davis and Callahan 1992, Sullivan 1994). The rodent's physiological tolerances, biochemical pathways, and morphological characters that permit its exploration and evaluation of its environment have been molded

through evolution. Its choice of habitat may be deeply rooted in its genotype (Wecker 1963, Drickamer 1972). Historical processes like these help explain the occurrence of species in a particular habitat type but less so its abundance. The number of individuals that inhabit a locality will more likely reflect ecological resources, behavioral decisions, physiological responses, and interactions with conspecifics and predators that occur during more recent time frames (Batzli 1992).

In the course of searching and choosing a place to settle, this hypothetical rodent must evaluate the condition of its environment. Evaluation and selection is likely mediated through the detection of proximate cues like scent trails, vegetative structure, or presence of food (Harris 1952, Drickamer 1972, Daly et al. 1980, Jannett 1981, Drickamer et al. 1992., Ferkin et al. 1995). Ideally, each individual must determine prior to settling (1) whether food, water, cover from the physical environment, mates, and any special resources are accessible in sufficient quantity and quality to survive and reproduce; (2) if there is sanctuary from predators or pathogens; (3) if the area is occupied by conspecifics, other competitors, or mutualistic species. Theory proposes that this individual should select a place to settle (i.e., its habitat) that will maximize its fitness (Rosensweig 1981).

The ultimate veracity of this individual's habitat choice will influence its fitness. However, decisions based on proximate cues may eventually render low fitness. As more individuals make their choices, local densities and habitat conditions change, thereby stimulating interactions among individuals which may act as feed-back mechanisms on population density (Christian 1971, M'Closkey 1981). At some levels of population density, individuals may select habitat because conspecifics are present (Ostfeld 1985, Ims 1987, Stamps 1991). The presence of like individuals may serve as an initial cue that

basic resources are present, mates are present, or that vigilance of predators can be increased. At higher densities, critical resources (e.g., food; effective cover) may diminish and predators may be attracted (Pearson 1985, Korpimäki and Norrdahl 1991). In turn, the risk of predation may influence habitat choices and foraging patterns of the individuals present (Desy et al. 1990, Lima and Dill 1990, Longland and Price 1991, Lagos et al. 1995, Korpimäki et al. 1996), and loss of food and increased predation may ultimately reduce or suppress population growth; the 'average' fitness in a population (Norrdahl and Korpimäki 1995, Korpimäki and Krebs 1996, Boonstra et al. 1998).

Further, initial cues may not indicate the presence of other species that share or inhibit the use of vital resources, particularly when the density of those species is low (Stapp and Van Horne 1996). The presence of other species may (Grant 1972, Redfield et al. 1977, Randall 1978, Dueser and Hallett 1979, Holbrook 1979b, Montgomery 1981, Hallett et al. 1983, Heske et al. 1996) or may not (Hallett et al. 1983, Morris 1983, Galindo and Krebs 1985, Vickery et al. 1989) influence habitat selection and abundance of rodents. As the abundance of different species fluctuates so may the spatial distributions of species, which in turn, will influence the intensity of interspecific interaction (Conely 1976, M'Closkey 1981, Hallett 1982, Llewellyn and Jenkins 1987). Likewise, the build-up of conspecifics may trigger aggressive defensive behavior and density-dependent feed backs on habitat selection, abundance, and fitness (Rosenzweig and Abramsky 1985, Morris 1987a; 1987b; 1989; 1996, Hallama and Dueser 1994). In general, interspecific competition may constrict a species' use of an area and or habitats thereby concentrating individuals (i.e., increasing density), whereas intraspecific competition may stimulate dispersion which will reduce density in a given area and promote use of different habitats

(Rosenzweig 1989, 1991; Wolff 1989).

The effects described above may be additive or compensatory on a rodent's underlying population processes (e.g., see Desy and Batzli 1989). Likewise, many of the effects may interact with density-independent influences like precipitation or temperature to shape a rodent's distribution and abundance (Vickery et al. 1989, Hörnfeldt 1994, Lewellen and Vessey 1998, Lima and Jaksić 1998). As these factors interact over time with individual habitat choices, spatial patterns in a species occurrence and abundance are created which exhibit properties at larger scales (e.g., metapopulations) that are equally pertinent to ecology and conservation (Gilpen and Hanski 1991, Pulliam and Danielson 1991). Consequently, the spatial and temporal scales at which distribution or abundance patterns are examined will dictate the types of processes that can be observed (Johnson 1980, Wiens et al. 1986, Morris 1987c).

This scenario provides some examples of how the choices of individuals in the process of habitat selection may ultimately determine the abundance of a population in a particular locality, and how the occurrence or abundance of a species may also be the consequence of complex interactions, including scales of observation (Fig. 2.1). Experiments and models can never capture all the interactions at all scales in such a system. Rather, one can only hope to identify major factors and predominant interactions at an appropriate scale (Gurney and Nisbet 1998, Addicott et al. 1987). Hence, the above scenario illustrates how predictive models of abundance based only on habitat affinities might lack explanatory power or even be misleading. What may prove more informative is an approach that quantifies habitat associations relative to other key factors that can also elicit responses in studied populations (Hilborn and Stearns 1982, Kaufman and

Kaufman 1989, Batzli 1992, Ives 1995, Ostfeld et al. 1996).

In this chapter, I take such an approach to better understand the influence habitat factors may have on abundance of five murid rodents occurring in the Sacramento Mountains, New Mexico. Herein, I first describe spatial and temporal patterns in the absolute abundance of these rodents over a six-year period. I then model relationships among potential causal factors and the abundance of each species. Findings of this study will be pertinent to at least one modern conservation issue: how to recover threatened populations of the Mexican spotted owl (*Strix occidentalis lucida*). The small mammals chosen for study comprise the owl's common prey (Ward and Block 1995, see below and Chapter 3). Knowledge regarding the factors influencing distribution and abundance of these small mammals is vital for understanding how Mexican spotted owls may respond to habitat disturbance or succession, and which habitat components, if any, can be manipulated to increase abundance of the owl's prey (USDI 1995).

The rodent assemblage of this study is comprised of five murid species and includes the deer mouse (*Peromyscus maniculatus*), brush mouse (*P. boylii*), Mexican vole (*Microtus mexicanus* = Mogollon vole [*Microtus mogollonensis*]; Frey and LaRue 1993), long-tailed vole (*M. longicaudus*), and Mexican woodrat (*Neotoma mexicana*). The geographic distribution and general habitat associations of these species in New Mexico has been summarized by Findley et al. (1975). Others have described habitat affinities of one or more of these species occurring at locations in the southwestern United States, beyond the Sacramento Mountains (Wilson 1968, Holbrook 1978; 1979a, Stinson 1978, Armstrong 1979, Cornely 1979, Goodwin and Hungerford 1979, Wilhelm 1979, Cornely et al. 1981, Honeycutt et al. 1981, Hubbard et al. 1983, Finley et al. 1986, Hoffmeister

1986, Svoboda et al. 1988, Suerda and Morrison 1998; 1999). Dice (1942) and Thompson and Hier (1981) briefly described occurrence of small mammal species among vegetation types north of the Sacramento Mountains, and Jorgensen et al. (1998) estimated indexes of habitat suitability for small mammals on Otero Mesa (a southern extension of the Sacramento Mountains). These studies were conducted in habitats different from those reported here and did not include either vole species. Conely (1976) reported densities and survival rates of both vole species occurring at one site in the Sacramento Mountains during two summers, one spring, and one fall. With this treatise, I describe spatial and temporal variation of absolute abundance of these rodents in a southwestern montane environment and present empirical models of processes that may influence changes in their abundance.

METHODS

Describing spatial and temporal variability in small mammal populations poses a descriptive problem that has a straight-forward solution: enumeration at multiple locations in an appropriately stratified environment with replication over time (Cody 1996). Disentangling the factors responsible for variability observed in small mammal abundance is more daunting. Here, I adopt an information-theoretic approach to identify predominant factors that likely influence the abundance of these five rodent species (Burnham and Anderson 1998). The approach has been used recently by Franklin et al. (2000) to delineate and quantify the relative importance of factors influencing life history traits of northern spotted owls (*S. o. caurina*). Following a brief description of the study area, I describe procedures used to stratify the environment, sample microhabitat features and small mammal populations, quantify variability in abundance, develop *a priori*

models of factors affecting small mammal abundance, and for selecting the most likely process models.

Study Area

This study was conducted in the Sacramento Mountains of south-central New Mexico. The majority of the study area was public land administered by the Sacramento Ranger District, Lincoln National Forest, USDA Forest Service (Fig. 2.2). The Sacramento Ranger District and in-holdings included 2,223 km^2 of land area (USDA Lincoln National Forest, *unpublished data*). Elevations ranged from 1300 m at the Tularosa Basin to a maximum of 2930 m at an unnamed summit east of Sunspot, New Mexico. Common soils included Cryoborolls (generally found from 2620 m to 2865 m in elevation), Argiborolls (2195 m to 2590 m), Ustorthents (2070 m to 2285 m), and Argiustolls (2010 m to 2135 m) (Ashford and Stury 1977).

During the study period (1991–1996), weather in the Sacramento Mountains varied over space and time. Average annual precipitation ranged from 31 cm in Alamogordo at 1326 m in elevation to 80 cm in Cloudcroft at 2652 m. Lapse of maximum temperatures over the same gradient averaged −0.75°C per 100-m gain in altitude. Annual precipitation at Cloudcroft ranged from 63 cm to 98 cm. Mean snow-depths during each measurable period (October–April) ranged 0.6 cm to 3.3 cm and averaged 1.8 cm over all six-years of study. Snow depths were below the six-year average during 27 of 42 (64%) measurable months. Seasonally, 60% of the annual precipitation fell during July–September and coincided with warm temperatures. During the six Junes, mean minimum and maximum temperatures ranged 4.6 °C to 7.6 °C and 21.4 °C to 24.3 °C, respectively. December mean minimum and maximum temperatures

ranged −7.0 °C to −4.9 °C and 3.6 °C to 6.9 °C, respectively. Daily temperatures fluctuated an average of 12 °C to 17 °C. In general, weather during the study period was similar to that in previous years except that significantly ($P < 0.05$) less snow accumulated during late fall and winter months and slightly (but not significantly) less precipitation fell during summer monsoons (see Chapter 1).

My research was limited to three broad "habitats" (*sensu* Hall et al. 1997) that were likely to be used by Mexican spotted owls or their prey and were categorized as mesic forest (MF), xeric forest (XF), or montane meadow (MM). I delineated these habitats according to broad vegetation associations (Dick-Peddie 1993), expected small mammal associations (Findley et al. 1975), and variation in environmental features (e.g., structural attributes of the vegetation, elevation, temperature) that could influence use of these habitats by the owl or its prey (Ganey and Dick 1995).

Vegetation in the mesic forest has been classified as Upper Montane Coniferous Forest by Moir (1993). This mixed-coniferous forest (>2280 m elevation) was dominated by Douglas-fir (*Psuedotsuga menziesii*) or white fir (*Abies concolor*). Vegetation in the xeric forest represented Lower Montane Coniferous Forest (2070–2590 m elevation) , and Coniferous Woodland (< 2070 m elevation; Moir 1993). Lower Montane Coniferous Forest was dominated by ponderosa pine (*Pinus ponderosa*). Conifer Woodlands were dominated by two-needle pinyon pine (*P. edulis*) or juniper (*Juniperus* spp.). Montane meadows included both the Montane Grassland described by USDA Forest Service (Lincoln National Forest Supervisor's Office, *unpublished data*) and wet meadows described by Dick-Peddie (1993). They occurred in valley bottoms > 2130 m elevation and were comprised of monocotyledon and herbaceous dicotyledon plants (grasses and

forbs), and scattered trees or shrubs along the periphery. This study area has been described further in Chapter 1 and by Kaufmann et al. (1998).

Sampling Design and Data Collection

I quantified habitat associations and temporal fluctuations of the five murid rodents using data gathered from stratified-random surveys. I stratified the study area into four broad categories. Three of these were the mesic forest, montane meadow, and xeric forest, as described above. The fourth category (OT) was comprised of all other vegetation communities not likely to be used by Mexican spotted owls (Dick-Peddie 1983) and included stands dominated by aspen (*Populus tremloides*), Montane Shrubland, or Desert Grassland (USDA Forest Service, Lincoln National Forest Supervisor's Office, *unpublished data*). I did not examine small mammal habitat associations and abundance in these other habitats.

Midway through the study, I partitioned the mesic forest habitat into two successional stages, a mid-seral stage (MF-M) dominated by conifers 60–100 yrs in age and a late seral stage (MF-L) dominated by conifers usually >200 yrs in age (Regan 1997). Conditions within the MF-M stage resulted from historical logging (Kaufmann et al. 1998) and resembled those described for montane coniferous stands of the Pacific Northwest undergoing late competitive exclusion or early understory reinitiation (Carey and Curtis 1996). Structural components associated with large-diameter trees and decadent stand conditions (i.e., snags; large decaying logs) were more prevalent in the MF-L. Although spatial extent of MF-L was very limited in the Sacramento Mountains (0.4–6.0% of the study area; Moline 1992), this seral stage was sampled to determine if microhabitat associations or abundance of small mammals differed significantly from that

found in the MF-M.

Site selection and replication. I conducted pilot sampling during the summer of 1991 to evaluate procedures for sampling small mammal populations. I also collected data to evaluate whether foraging male owls increased spatial variability in prey abundance by depleting small mammal numbers at frequently hunted patches (Carey et al. 1992, Ward and Block 1992). Data from four of the eight pilot-study sites were included in analyses reported here. These four sites represented the area closest to an owl roost center or nest and thus approximated the site selection procedures used in 1992 (described below). Two of the four sites were in the MF-M habitat and two were in XF habitat (Fig. 2.2). Montane meadows and MF-L sites were not sampled in 1991.

The pilot work of 1991 did not support the hypothesis that spotted owls increased spatial variability in abundance of their common prey through depletion (Ward and Block 1992). Thus, in sampling these small mammal populations I felt justified in stratifying the owl's local environment according to habitat, independent of the owl's hunting frequency. I selected the sites sampled during 1992 through 1996 at random from a list of 102 possible owl territories documented since 1986 (USDA Forest Service, Sacramento Ranger District, *unpublished data*) with two constraints. Each site had to be (1) within a habitat patch large enough to include a live-trapping grid with minimal edge effects and (2) <0.8 km from a recently occupied nest or roost center. The specific sampling area was placed as close to an owl's nest or roost as possible while remaining within habitat boundaries. Thus, the specific habitat patch sampled was not selected from a random list but rather according to juxtaposition to a randomly selected owl use-center. These conditions were imposed to be reasonably sure that the sampled habitat was available to

spotted owls for hunting.

I selected 18 sites, six in each of three habitats (MF-M, MM, XF) for sampling small mammal populations and microhabitat features (Fig. 2.2). A particular site was only sampled once during a given summer. All sites were sampled during the summers of 1992 and 1993. One original MF-M site was not sampled during the summer of 1994 and two MF-L sites were established and then sampled during 1994 and 1995. Only twelve and four of 20 possible sites were sampled in the summer of 1995 and 1996, respectively, because of limited funding (Table 2.1). When sites had to be eliminated in 1995, those that previously produced the maximum range of variation in small mammal abundance within each habitat were retained. During 1996, only one site in each habitat could be sampled.

Additional sampling was conducted to estimate seasonal variation in abundance of these rodents. Accordingly, two of the original six sites in each of the three habitats were sampled once, quarterly between 1993 and 1994 (Table 2.1). Of the possible sites that could be sampled, those with the greatest chance of winter access were selected.

Rodent microhabitat. To characterize habitat types and quantify microhabitat associations of small mammals, I measured 30 environmental attributes in the vicinity of live-trapping stations (Table 2.2). This suite of variables was considered necessary to describe site conditions and included structures likely used by small mammals. However, only a small subset of the 30 variables were used to model abundance factors, and variable inclusion was based on a priori reasoning (see Model development below). Every station was sampled once during the study (June through August). Except at the two late-seral mesic-forest sites, a subset of all stations from each grid was sampled in

two or three consecutive summers during a similar period (1992–1994; Table 2.1). Microhabitat features were sampled from all stations at the two MF-L sites during the summer of 1994. I used four different sampling procedures to measure microhabitat variables: point, line-intercept, fixed-area plot, and variable-radius plot methods (Bonham 1989; Table 2.2).

Each trap-station marker provided a fixed reference point for sampling the environmental attributes. In total, this provided a random-systematic sample of environmental attributes from each site. I measured two variables that described site physiography, slope (%), and elevation (nearest 10 ft converted to m) directly from each trap-station marker using a clinometer and altimeter, respectively (Table 2.2).

I used a 10-m line intercept to sample several variables related to ground cover (Table 2.2). This line was established by placing a meter-tape in a random direction and centered on each trap-station marker. Each cover variable was tallied as present (1) or absent (0) at each of the ten 1-m points. Percent cover was calculated as the tally sums multiplied by 10. Litter depth (cm), an index of soil condition and past site productivity, was measured by pushing a pointed rod through the soil organic horizon at each intercept point until meeting firm resistence and recording the distance with a ruler. Height (cm) of the tallest grass stem or forb leaf, an index of vertical cover and above-ground, primary productivity, at each intercept point was measured with a cloth-tape. Litter depth and grass-forb height values were averaged over the 10 points.

I used a circular plot (5-m radius; 78.5 m^2) for estimating shrub, sapling density (no/ha), log density, and indexing volume of downed wood (m^3). These variables provided indexes of the amount of cover and food plants potentially used by some of the

small mammals. A plot was centered on each trap-station marker and circumscribed around the original 10-m line intercept and a second perpendicular line (also 10 m in length). Within the plot, all shrubs >0.5 m tall and saplings (>0.5 m tall and <10.0 cm dbh) were counted and recorded by species. Tree stumps (potential burrow sites for some rodents) were also counted. The length (m) and center-point diameter (cm) of all logs ≥10-cm diameter and >2 m length occurring in the plots were measured with a meter tape. The product of log length, one half of the center-point diameter, and π was used as an index of the volume of small (10 – 30 cm) and large (>30 cm) logs in four decomposition states: (1) intact with most to all of bark attached; (2) intact with less than half of the bark remaining; (3) intact with no bark remaining; (4) no longer intact and showing external signs of decay and deterioration. Length of stage-5 logs that had decayed to linear forms of debris was also measured.

I used a variable-radius plot method (see Bonham 1989:177) to sample live and dead trees (≥10 cm dbh and ≥2 m tall). At each trap-station marker, trees were tallied using a cruise angle with a 20 basal-area factor. When peering through this device held at a standard distance from plot center, trees with boles that exceeded the limits of the angle were counted for the plot (e.g., Bonham 1989:30). The species and dbh (in cm using a metric diameter tape) of each counted tree was recorded. Basal area (m^2/ha) and density (stems/ha) of trees were calculated following (Bell and Dilworth 1989).

Weather. I included two weather factors, cumulative precipitation (cm) and mean minimum temperature (°C) during specific periods for modeling rodent abundance. Predictive equations and associated measures of reliability are given in Appendix 2.A.

Rodent abundance. I sampled the populations of the five rodent species to

estimate absolute abundance (density as no./ha; $\hat{D}$) using closed-population models (Otis et al. 1978, White et al. 1982, Rexstad and Burnham 1991). The sampling design followed a mark-recapture framework and trapping procedures were developed to obtain maximum numbers of marked individuals while meeting the assumption of demographic closure (White et al. 1982). This approach required substantial effort at the cost of site replication. However, the approach was deemed necessary because other procedures (see reviews in Caughley 1976, Seber 1982) typically provide only relative estimates and indexes of abundance that typically do not permit extrapolation to absolute abundance and do not provide an estimate of enumeration error (White et al. 1982, Xia and Boonstra 1992, but see Hanski et al. 1994).

I used large (7.5 x 8.8 x 22.5 cm) and extra-large (10.0 x 11.2 x 37.5 cm) Sherman live traps (H. B. Sherman Co., Tallahassee, FL) to capture small mammals. Two sizes of traps were used to allow for any trap preference by larger rodents like woodrats. However, the largest traps were set to capture the smaller rodents like mice. Number and arrangement of live traps at a site varied slightly in 1991 compared to other years, and between forest and meadow habitats during all years.

At each site sampled in 1991, I used 100 large traps placed 20 m apart and arranged in a 10 x 10-station grid (3.24 ha) nested within a 10 x 10-station grid of 100 extra-large traps placed 40 m apart (grid area = 12.96 ha). I established two sizes of grid to evaluate trap spacing effects on capture rates (Ward and Block 1992). Traps were baited with a mixture of peanut butter, rolled oats, and chicken feed, provided with coarse-grade cotton bedding, and covered with wooden shingles to insulate animals from extreme temperatures and rain. Traps were set for 10 consecutive nights and checked

each subsequent morning. Traps were shut with bait placed outside of each trap (pre-baiting) for one night prior to initiation of each trapping session to accustom animals to the presence of traps and improve capture success. Trapping was conducted during July and August in the two forested habitats only. These sites were not sampled concurrently.

During 1992 through 1996, I increased the number of large traps placed in forested habitats to 121 and reduced the number of extra-large traps to 36 and arranged them as an 11 x 11- and 6 x 6-grid, respectively. Both grids were nested with the same spacing between trap-stations as in 1991, producing a grid area of 4.0 ha. The changes appeared warranted given the numbers of individuals captured in 1991 (Ward and Block 1992). Consequently, I analyzed data collected from only the nested portion of the grids sampled in 1991 (a 3.24 ha grid with 100 large and 25 extra large traps) to maintain comparability with data sets collected during 1992–1996.

Beginning in 1992, I also sampled small mammal abundance in meadows using 105 large traps placed 15 m apart and arranged in a 5 x 21-station grid (1.8 ha). Traps were placed at a closer distance because the species most likely to be captured (e.g., voles) were expected to attain higher densities and exhibit closer spacing than those species dwelling in the forest habitat types (Stickel 1968, Conely 1976, Madison 1985). Extra-large traps were not used because the larger rodents encountered in the forests were not expected to use meadows (Findley et al. 1975). I used a rectangular grid to conform to the linear shape of the meadows.

Also beginning in 1992, at least one replicate of a given habitat was sampled concurrently with replicates of the other habitats. During a sampling occasion, traps were pre-baited for one night then left open for eight consecutive days. In addition to bait and

bedding described above, I added fresh forbs and grasses to traps to prevent dehydration of captured voles (Van Horne 1983). Traps in all habitats were placed near suspected burrows, run-ways, or cover within 5 m of trap stations and moved periodically to increase capture success. All traps were checked twice each day, once in the morning and again prior to dusk.

Once captured, species and individuals were identified, marked with uniquely numbered tags (National Band and Tag, Co., Newport, KY) in both ears, weighed with spring-scales to the nearest 0.5 g (Pesola, Switzerland), classified according to gender, age using pelage coloration and size, and reproductive state using appearance of genitalia and mammary glands, measured (length of tail, head and body, ear, hind foot, all in mm), and released at the site. A set of voucher specimens were sent to Museum of Southwestern Biology, Albuquerque, New Mexico, to verify field identification of commonly captured rodents. Hypothermic or animals in torpor were held temporarily and treated by warming them slowly prior to release at the capture site. Following outbreaks of hanta-virus in northwestern New Mexico in 1993, data collectors were provided with specialized equipment and trained in the procedures recommended for handling wild rodents in a field setting (Childs et al. 1995, Mills et al. 1995). All animal handling and treatment procedures conformed to professional guidelines (National Academy of Sciences 1996, American Society of Mammalogists 1998). Trapping procedures were approved by Animal Care and Use Committee of Colorado State University (Protocol 92-127A-02).

Each site was trapped once during mid-July through mid-August of each year. This period coincided with high activity and numbers of rodent species of interest and the

period when spotted owls would be feeding young (Conley 1976, Van Horne 1981, Taitt and Krebs 1985, Drost and Fellers 1991, Rinkevich et al. 1995). Although small mammal populations are customarily sampled monthly or bi-annually, this single sampling period provided the best benchmark for annual population trends given the study objectives and inclement conditions imposed by the study area. Other investigators have referenced the average number captured between spring and fall trapping sessions to examine owl responses to small mammal populations (Lundberg 1981, Rohner et al. 1995). By using summer values, I approximated the mid-point between minimum numbers of rodents encountered during spring and maximum numbers during early fall.

Nonetheless, to describe seasonal shifts in abundance within a single year, I also sampled two sites in each habitat during one fall (1993), winter (1994), and spring (1994) period. Trapping procedures were slightly modified during non-summer periods to allow for inclement weather (Schmid 1984). Large Sherman traps were placed within 18.9-liter plastic buckets at each trapping station. Extra-large traps were not used. Three holes were drilled into the vertical face of the bucket near the bottom. One 5-cm hole was created to provide a direct entrance into an enclosed live trap. Two 2.5-cm holes were offset approximately 45° from the main entrance to provide alternate entrances to the enclosed trap. Each enclosed trap was surrounded by cotton and each bucket was sealed with a plastic lid to further insulate captured animals. All other trapping and animal handling procedures described previously were followed.

Data Analysis

I used two approaches to analyze the distribution and abundance of the five rodent species. First, I summarized spatial and temporal patterns using parametric

statistics. Second, I used an information-theoretic approach to model habitat-abundance relationships within the context of other biotic and abiotic interactions.

Distribution and Abundance. I used biomass per unit of area ($\hat{B}$; g/ha), the product of average mass ($\overline{mass}$) and density ($\hat{D}$), to describe patterns in rodent distribution and abundance. An associated sampling error was estimated using the Goodman's (1960) approximation,

$$\hat{var}[\hat{B}_{ijkt}] = (\overline{mass}^2_{ijkt} \bullet \hat{var}[\hat{D}_{ijkt}]) + (\hat{D}^2_{ijkt} \bullet \hat{var}[\overline{mass}_{ijkt}]) - (\hat{var}[\overline{mass}_{ijkt}] \bullet \hat{var}[\hat{D}_{ijkt}]) \quad (2.1)$$

where $\overline{mass}_{ijkt}$ is the average body mass of species *i* at site *j* of habitat *k* at time (year or season) *t*, $\hat{D}$ is density, and $\hat{var}$ is the estimated sampling variance. Estimates of the sampling variance of $\hat{B}$ were used to describe the precision of $\hat{B}$ and for making statistical comparisons when site replication was limited. I chose to summarize abundance using $\hat{B}$ because this measure provided more information about the abundance of food for the Mexican spotted owl compared to prey density. I also present the distribution of naive density and $\hat{D}$ to compare my results with other studies that report density of these five species. I calculated naive density as number of individuals of a species encountered at a given site divided by area (ha) of the trapping grid. Procedures used to estimate $\hat{D}$ are described below.

I accounted for multiple sources of variation in my estimates of rodent abundance. Total variation observed in $\hat{B}$ is a function of ecological process and sampling. For example, variance of biomass of species *i* averaged over all sites and years within a given

habitat *k*, would include two forms of process variation, that caused by differences associated with site quality and that caused by time-related factors (e.g., changes in weather). It would also include two forms of sampling variation, one caused by selecting a different set of sites (or rodent subpopulations) to sample and another caused by capturing a different subset of individuals within a subpopulation. For clarity, I refer to the latter source of sampling variation as enumeration error.

In the above example, among-site variation in $\hat{B}$ would be treated as sampling variation when testing for temporal process variation in $\hat{B}$ within a habitat type. This approach provides a conservative (under) estimate of total process variation (σ^2) because among-site variation includes some spatial process variation in addition to sampling variation. It is also important to note that in conventional analyses, enumeration error is often ignored and presumed less than or equal to among-site variation. However, if an estimator is imprecise, average enumeration error could be greater than among-site variation, and consequently the amount of temporal process variation estimated from a data set would be exaggerated. Thus, I strived to estimate enumeration error and evaluate its magnitude, when possible. I used a coefficient of variation of biomass to describe the magnitude of enumeration error. For the habitat specific case,

$$CV_{ik} = (\overline{SE}_e[\vec{B}_{ik}] \;/\; \vec{B}_{ik}) \cdot 100\% \qquad (2.2)$$

where

$$\vec{B}_{ik} = \sum_{j=1}^{s}\sum_{t=1}^{m} \hat{B}_{ijkt} \;/\; K \qquad (2.3),$$

$$\overline{SE}_e[\hat{B}_{ik}] = \sqrt{\sum_{j=1}^{s}\sum_{t=1}^{m} \hat{var}_e[\hat{B}_{ijkt}] \;/\; K^2} \qquad (2.4),$$

and *K* is the total number of sites (*s*) and years (*m*) sampled (Burnham et al. 1987). Very precise estimates would be ≤10%.

Reliable estimates of rodent biomass required unbiased, precise estimates of rodent mass and density. To obtain reliable measures of mass, field weighing procedures were monitored and spring scales were calibrated regularly with known measures of mass. I assumed that capture of individuals provided a representative sample of mass in these rodent populations. Density (*N*/ha) was estimated from mark-recapture data. I used Program CAPTURE to estimate population size at the beginning of a given trap session ($\hat{N}$) from the proportion of the population initially captured ($\hat{p}$) or recaptured ($\hat{c}$) in a given sample, and for estimating the average maximum distance moved (m) by marked individuals (Otis et al.1978, Rexstad and Burnham 1991). This distance was used to determine an effective sampling area (Stickel 1954, Otis et al. 1978).

To estimate N_{ijkl}, nine possible (closed-population) models representing different assumptions about small mammal responses to capture were tested for fit to a given set of data (Rexstad and Burnham 1991:18). A discriminant function was then used to select the most appropriate model. Obtaining reliable estimates of density under this procedure required that (1) adequate numbers of individuals were marked, (2) the sampled population was closed to demographic processes, (3) the proper estimator was selected from a suite of estimation models, and (4) the appropriate area ($\hat{A}_E$) occupied by the sampled population was determined.

I developed sampling and data-collection protocols to maximize captures as discussed previously. Nonetheless, estimates of enumeration errors can be biased when

inadequate numbers of individuals are marked (~200) or capture probabilities per trapping occasion are low (<0.30) because an inappropriate estimator may be selected (White et al. 1982, Menkens and Anderson 1988). Other methods have been suggested for estimating *N* when small numbers of individuals are captured (Menkens and Anderson 1988). However, these procedures require that capture probabilities be constant or only change with time and rely on subjective screening of initial CAPTURE results and pooling of data over trapping occasions. I chose to be consistent and less subjective by using Program CAPTURE to estimate density and enumeration errors for all data sets except when the number of individuals marked was <3. In the latter cases, I substituted naive density. Pilot research showed that when numbers of marked individuals were low, naive densities were comparable to $\hat{D}$ (Ward and Block 1992).

I attempted to assure demographic closure through sampling procedures (see above). Program CAPTURE provides a test of the demographic closure assumption (Otis et al. 1978). However, this test has limited power for properly rejecting a null hypothesis of closure (Rexstad and Burnham 1991). Given the limited power and large number of data sets examined, I did not use this test. Rather, I assumed that by minimizing trap mortalities, restricting the duration of sampling, and accounting for an expanded sampling area I would limit the influences of immigration, births, deaths, and emigration to near zero. Mortalities that did occur were removed from the modeling procedure and added afterwards to resulting CAPTURE estimates of *N*. If my assumptions about closure were incorrect, then density would be underestimated (when immigration or births occurred) or overestimated (when deaths or emigration occurred).

To be consistent and objective in modeling a large number of data sets, I relied

primarily on the ranking procedure of Program CAPTURE when choosing the most appropriate model. There were two conditions where I used different models. First, if the most appropriate model selected was based on temporal, behavioral, and heterogeneous responses to capture (model M_{tbh}), I selected the next highest ranked model. If rankings from two or more models were close, I chose a model by evaluating the series of goodness of fit tests offered in Program CAPTURE (White et al. 1982) and, if that failed to distinguish an appropriate model, I used the model type commonly selected in analyses of other data sets of the same species.

The area of a trapping grid is an underestimate of the area occupied by a sampled population and its use in calculations will lead to an overestimate of density. I therefore estimated an effective sampling area ($\hat{A}_E$) from the grid dimensions and a boundary strip (W) taken as half the mean maximum distance moved by individuals between successive capture locations (Otis et al. 1978:73),

$$\hat{A}_E = A_G[1 + a\tilde{W} + b\tilde{W}^2] \tag{2.5}$$

where A_G is the area within the trapping grid, a is ratio of perimeter to grid area, and b is the ratio of π to grid area. The sampling variance of $\tilde{W}$ for each grid is estimated from the sampling variance of mean maximum distance moved within a grid and is incorporated into estimates of enumeration error of density for that site,

$$\hat{var}_e[\hat{D}] = \hat{var}_e[\hat{N}]/\hat{A}_E^2 + \hat{D}^2[(a + 2b\tilde{W})/(1 + a\tilde{W} + b\tilde{W}^2)]^2 \bullet \hat{var}_e[\tilde{W}] \tag{2.6}$$

where $\hat{var}_e[\hat{N}]$ is the enumeration error of population size estimated with Program CAPTURE. Use of the procedure assumes that the maximum distance moved

approximates the radius of an average home-range area during the sampling period (Stickel 1954).

I described patterns in the abundance of these five rodents in two ways. First, I summarized spatial and temporal patterns in biomass using parametric statistics. Second, I estimated the significance of temporal and spatial process variation in biomass of each species. I summarized spatial variation by averaging $\hat{B}$ of each rodent species over site replicates (*j*) and the six summer periods (*t*), and then by reporting this mean value according to habitat type (*k*). In this case, average enumeration errors $\overline{\overline{SE}}_e$ (Equation 2.3) associated with this mean were reported as a source of sampling variation. Although these mean abundance values ($\hat{\bar{B}}_{ik}$) mask primary sources of variation (e.g., annual variation in biomass), they provided a concise summary of the distribution and abundance of the five rodent species across macrohabitats. I described temporal (annual and seasonal) trends in biomass of each species as means estimated among sites within the same habitat type and reported the within habitat averages by year or season ($\hat{\bar{B}}_{ik}$). In this case, variation among sites was used to report sampling variation associated with $\hat{\bar{B}}_{ik}$.

I tested for significant spatial (among habitat) and temporal (among summers) variation in biomass of each species using a mixed-effects model (Littel et al. 1996). In this analysis, I used a subset of the data that included the same sites in each habitat (MF-M=3, MM=3, XF=4 sites) that were sampled during each summer in 1992 through 1995. I treated data from each year as a repeated measure of each randomly assigned site. Year

and habitat type were considered fixed effects. I assumed that the variance-covariance matrix was unstructured (Appendix 2.B; SAS Institute Inc.1996).

I examined the extent of variation in biomass of each species in 1991–1992 and 1995–1996 in separate tests because the locations of sampling differed (1991) or replication was limited to one site (1996). I compared habitat specific values of annual biomass ($\hat{\bar{B}}_{ik}$) for each species in 1991 to that in 1992, and $\hat{\bar{B}}_{ik}$ from 1996 to that in 1995 using a Z-test (White et al. 1982:139). I used the average enumeration error as a measure of sampling variation in these tests. Hence, any inferences stemming from these tests are limited to the specific populations examined. Significant results from these separate tests would indicate if there was additional temporal variation in biomass beyond that demonstrated for the period 1992–1995.

I also used separate tests for variation of biomass in the two seral stages of mesic forest because of unequal replication among years. Sampling of rodent abundance was replicated in both seral stages during 1994 and 1995, but not in 1996. Thus, biomass of each species occurring in mid-seral and late-seral stages during the summers of 1994 and 1995 were compared using a repeated measures, mixed model. The analogous comparisons for data from 1995 and 1996 were made using a Z-test.

Factors affecting rodent abundance. I followed the information-theoretic (I-T) philosophy proposed by Burnham and Anderson (1998) to model factors that likely influenced abundance ($\hat{B}_{ijt}$) of each rodent species. A primary purpose of this analysis was to identify microhabitat components that could serve as target variables in future manipulations designed to elicit increases in these rodent populations. The analysis

entailed (1) developing *a priori* global and subset (candidate) models given existing theory and empirical information that described potential causes of increase in each rodent's abundance; (2) estimating parameters and associated variances in each candidate model using a statistical technique appropriate to collected data and the theory of maximum likelihood; (3) selecting among the candidate models using a theoretically based criterion that balances bias and precision and corrects for small sample size. When a global model exhibits some reasonable level of fit to the data, then the variables of the best (i.e., most parsimonious) model or set of models may be inferred to be the most likely factors influencing the studied response, given the data collected (Burnham and Anderson 1998). Moreover, model uncertainty (i.e., the potential for variation in model structure given analysis of different data sets) can be accounted for by estimating average parameter values and associated variances across models. Under this approach, it is also possible to weight the likelihood of including a given parameter in a "best" model. Thus, I used this model-selection paradigm to evaluate the importance of microhabitat components on abundance of each rodent relative to other potentially important factors (e.g., weather; interference competition).

The I-T approach provides stronger inferences compared to traditional methods of model selection that are based on statistical hypothesis tests. Following this approach requires development of multiple, well contemplated, alternative or competing explanations prior to evaluation of data. It has been argued elsewhere that such a philosophy is necessary for promoting strong inference (Chamberlin 1890, Platt 1964). The practice of massaging the same data repeatedly for patterns or for *a posteriori* explanations and the use of traditional approaches for selecting appropriate models run a

greater risk of producing spurious results (Burnham and Anderson 1998, Anderson et al. 2000). Because any habitat factors identified herein could be targeted in future experimental manipulations of public land, I desired procedures that would permit the most reliable inferences given the study design and data at hand. Accordingly, I chose the I-T approach over more traditional procedures of model development and selection.

Model development: To develop global and candidate models in a standardized fashion, I first constructed envirograms of each rodent species (Figs. 2.3–2.7). Envirograms hypothesize the ecological linkages among direct and indirect factors and abundance of a species at a particular time and place (Adrewartha and Birch 1984). These ecological flow-charts are developed using standardized conceptual framework following the logic and terminology embodied by Adrewartha and Birch's (1984) Theory of Environment. Others have also found envirograms useful for conceptualizing wildlife-habitat relationships or for guiding quantitative assessments of environmental effects (Van Horne and Wiens 1991, James et al. 1997, Patton 1997).

Envirograms depict each organism within the context of a *centrum* and a *web*. The centrum is comprised of factors that directly affect an organism's abundance. Direct effects are categorized as resources, predators, "malentities," or mates. Resources are environmental components that enhance an organism's chance of survival and reproduction and are either negatively or not influenced by the abundance of the organism (e.g., the organism's food). Predators reduce survival and reproduction in the focal population, and in turn, benefit from increases in the organism's abundance. Malentities reduce survival and reproduction in a population but are not affected by the organism's abundance (e.g., excessive temperature). Mates convey a positive-positive relationship.

Indirect factors comprise the *web* and include anything that can affect a species by modifying its centrum, including the effect of individuals of the focal species on their own population (e.g., density-dependent effects). Flow in an envirogram tends from distal indirect influences in the web toward the most proximate direct effects on the organism's population shown in the centrum.

The number of factors and interactions depicted in an envirogram are limited only by knowledge of the organism's ecology. I constructed species-specific envirograms from results of experimental and observational studies reported in the literature. When possible, I limited the information used to develop the envirogram to studies on the focal species occurring in montane meadows and/or coniferous forests or woodlands. If information pertaining to a species' ecology was limited or lacking, I used information from studies on other related species. No envirogram was expected to be comprehensive. However, envirograms developed for this study included more effects and factors than could be sampled and ultimately modeled. Thus, in addition to providing a template for developing statistical models, the envirograms provided a schematic of possible interactions that served as alternative explanations or topics for further investigation. In this sense, envirograms were useful for portraying the relevance of modeled factors within the greater realm of ecological complexity.

I used three levels of indirect factors to depict the web portion of each envirogram (Fig. 2.3–2.7). As one might expect, direct and indirect factors varied among the five species according to their respective ecologies and the availability of scientific literature. The scientific basis and assumptions specific to each envirogram, and the deduction of quantitative models from the envirograms, are discussed below.

Deer mouse—Food and water are obvious resources that can influence abundance of deer mice (Fig. 2.3). Deer mice are generally omnivorous but rely on some foods seasonally (Cogshall 1928, Baker 1968, Merritt and Merritt 1980). In coniferous forests or woodlands, deer mice usually consume arthropods and seeds of herbaceous plants during spring and early summer periods (Jameson 1952, Vaughan 1974, Holbrook 1978, Goodwin and Hungerford 1979, Van Horne 1982a, Haufler and Nagy 1984) but may also consume conifer seeds and green vegetation during spring months at high elevations (Williams 1959, Merritt and Merritt 1980). During late summer and early fall periods, deer mice shift their consumption to conifer seeds, fruits, and sometimes to fungus (Jameson 1952, Williams 1959, Williams and Finney 1964, Merritt and Merritt 1980, Rhoades 1986, Maser and Maser 1987). Conifer seeds and other forms of mast become the primary food throughout the fall and winter (Jameson 1952). Deer mice are moderately efficient in maintaining water balance (MacMillen 1983). Although these mice meet some of their water requirements during metabolism of food, water is sometimes obtained from other sources, including ice, snow, or condensation (Howard 1951, Stebbins 1977).

Increases in food within conifer forests or woodlands, particularly an ample, fall seed crop, can increase abundance of deer mice by (1) enhancing overwinter survival and body condition prior to the next breeding period, (2) enticing immigrants to settle, and (3) permitting early and extended reproduction (Jameson 1953, Fordham 1971, Gashwiller 1979, Gilbert and Krebs 1981, Taitt 1981, Halvorson 1982, Van Horne 1982a, Teferi and Millar 1994, Morrison and Hall 1998). Under laboratory conditions, lack of food and water can reduce weight and survival of juvenile deer mice (Porter and Busch 1978).

Lack of water alone can also inhibit reproduction (Lindeborg 1948, Nelson and Desjardins 1987).

Food and water supplies for deer mice are, in turn, influenced by several environmental interactions (Fig. 2.3). For example, abundance and reproduction in many arthropods and fungi are influenced by interactions among substrate, vegetative cover, solar radiation, air temperature, and precipitation from a preceding season (Cooke 1979, Marra and Edmonds 1998, Speight et al. 1999). In particular, large decaying logs provide prime habitats for arthropods and fungi by storing moisture and prolonging favorable humidity and temperature levels (Maser and Trappe 1984, Speight et al. 1999). Plant productivity depends on similar environmental interactions but also on the types and sizes of plants in the area. For example, growth and reproduction in montane herbaceous plants will depend in part on spring temperatures and soil moisture levels (Vaughn 1974, Harper 1977, Walker et al. 1994). The latter will be influenced by winter snow packs or early spring rainfall. Reproduction in perennial forms will also depend on nutrients stored during a previous growing season, which is affected by plant size and age (Harper 1977). Similarly, older, larger shrubs and trees with fuller canopies generally produce more seeds (prior to senescence) than younger, smaller individuals (Barnes et al. 1998). Amount of woody debris and abundance of conifer or mast producing species present will also be influenced by the type of plant community occurring at a particular site and its stage of development. Some disturbances (e.g, fire; logging) remove components that relate to important food sources of deer mice and yet this mouse may still increase in numbers (Halvorson 1982, Kirkland 1990). The contradiction can be explained as an increase in accessability of seeds from conifers adjacent to harvested or burned areas,

increased production of understory plants that can provide some food and cover, and a reduction of the mouse's competitors (Gashwiler 1969, Halvorson 1982).

Given the role of fall food sources for increases in deer mouse abundance, factors stimulating large crops of conifer seeds seem particularly germane (Fig. 2.3). Production of large conifer-seed crops or oak masting will vary temporally and among tree species according to different reproductive cycles and limiting agents (Barnes et al. 1998). For instance, seed fall by Douglas-fir is somewhat irregular with one heavy and one medium crop occurring approximately every seven years (Burns and Honkala 1990). Seeds drop primarily in September through November and require two previous spring-summer periods to develop and mature (Owens 1973). Deep frost during development of Douglas-fir primordia (first winter) and insect damage during later periods can limit seed development and viability (Owens 1973). In contrast, large seed crops for white fir, ponderosa pine and pinyon pine occur every 3 to 9 years, 3 to 4 years, or 4 to 7 years, respectively (Burns and Honkala 1990). Seeds from these tree species also drop primarily from September to November. However, white fir seeds drop from cones developed during the preceding spring-summer and seed production can be limited by damage from insects, late snows, or strong winds of the same year (Burns and Honkala 1990). Ponderosa pine seeds take two spring-summer seasons to develop and seed development may be inhibited by pollination in the first spring and freezing weather in the subsequent winter (Burns and Honkala 1990). Pinyon pines take nearly three summers to develop and mature, and seed production may be limited by conditions that inhibit pollination, freezing temperatures, insects, and lack of adequate moisture (Burns and Honkala 1990). In addition, production and release of oak mast may or may not be synchronous among

species in a local environment (Sork et al. 1993, Koenig et al. 1994). Factors affecting mast production include number and size of mast producing species, suitable conditions for successful pollination and seed set, warm spring temperatures, adequate summer moisture, and adequate time since last masting (Sork et al. 1993, Koenig et al. 1994). Thus, irruptions of deer mice may be linked to instances when environmental conditions and internal timing allow multiple tree species to produce and drop large seed crops simultaneously. These conditions are supposedly dry, moderately windy periods during pollination (late spring), adequate rainfall and hence moist soils during growing seasons when seeds are developing (spring and/or summer), and mild winter temperatures that limit loss of reproductive structures.

Inter- and intraspecific interactions may also affect the amount of food or water available to deer mice (Fig. 2.3). For example, Smyth (1966) found that early snow cover following seed drop can protect food resources of ground foraging granivores from seed-eating birds. In some situations, brush mice or microtine rodents may exploit similar resources or, through interference, cause individual deer mice to use different habitats where certain foods and water may be less available (Brown 1964a, Grant 1972, Redfield et al. 1977, Holbrook 1979b, Cranford 1984, Belk et al. 1988, Schulte-Hostedde and Brooks 1997). It is also possible that aggression by adult female deer mice defending young may indirectly exclude adjacent conspecific individuals from accessing key resources (Wolff 1985a). Finally, large numbers of deer mice during a given fall may diminish food supplies leading to emigration, low overwinter survival, and low reproduction in the subsequent spring (Van Horne 1982a, Millar 1984, Drost and Fellers 1991, Millar and Teferi 1993). Any of these latter processes could decrease abundance of

deer mice in a given area.

The availability of females capable of breeding may also have a strong influence on summer abundance of deer mice (Fig. 2.3). Although environmental conditions may sometimes lead to increased litter size (Layne 1968, Millar 1989) or extended breeding seasons (Wunder and Byman 1979, Millar 1989), the number of reproducing females in the population is likely to have a greater influence on population increase (Christian 1971).

The number of females available for reproducing during a given breeding season is likely influenced by a myriad of factors, including quality and quantify of food or other habitat conditions (like cover or nesting sites), density of conspecifics, and social behavior and organization. The influence of all but the latter factors on numbers of reproducing females likely parallel those for general deer mice numbers discussed above and below. Social factors, however, are thought to regulate deer mice populations within the limits of carrying capacity (Kaufman and Kaufman 1989). Deer mice usually mate promiscuously (Wolff 1989). Males are believed to compete for females, and females compete for resources to raise young. The latter are usually territorial and aggressive in defense of nest sites and/or young (Wolff 1985a; 1993). Non-breeding individuals, particularly subadult individuals may be tolerated in closer proximity by breeding females. At high densities, particularly late in the breeding season, delayed maturation may permit access of resources necessary for overwinter survival to non-breeding individuals. The reduction in reproducers through delayed or cessation of reproduction will lead to population decline as seasonal mortality sets in (Terman 1968, Drost and Fellers 1991). In contrast, when subadult females can disperse away from territorial

adults, find suitable resources and mature, additional reproducers will become available. Accordingly, the effects of social behavior on maturation of females can play a pivotal role in population dynamics of deer mice (Kaufman and Kaufman 1989).

Predators decrease abundance of deer mice by direct removal (Fig. 2.3; Drost and Fellers 1991), or contribute indirectly to deer mouse increase by reducing effects of interspecific competitors (Kotler and Holt 1989). There are a number of predators of deer mice in the Sacramento Mountains including various species of snakes (western rattlesnake [*Crotalis viridis*], gopher snake [*Pituophis melanoleucus*]), mammals (coyote [*Canis latrans*], gray fox [*Urocyon cinereoargenteus*], long-tailed weasel [*Mustela frenata*], stripped skunk [*Mephitis mephitis*], spotted skunk [*Spilogale gracilis*], bobcat [*Lynx rufus*], racoon [*Procyon lotor*], and ringtail cat [*Bassariscus astutus*]), and birds (common raven [*Corvus corax*], red-tailed hawk [*Buteo jamaicensis*], American kestrel [*Falco sparverius*], western screech owl [*Otus kennicottii*], northern saw-whet owl [*Aegolius acadicus*], and flammulated owl [*Otus flammeolus*]), particularly Mexican spotted owls. The extent of predation may be dependent on the abundance of other prey species or food resources. However, predation of deer mice specifically by Mexican spotted owls does not appear to be influenced by abundance of alternative prey (see Chapter 3). Dense understory vegetation, logs and woody debris, burrows, and snow cover may limit predation on deer mice (e.g., see Planz and Kirkland 1992, Hayes and Cross 1987). Availability of these forms of cover is affected, respectively, by the type and successional stage of a vegetation community, soil texture, soil particle size, and weather events. Disturbance can influence cover by direct removal of components, addition of components, or indirectly by affecting plant community composition and

structure (e.g., see Halvorson 1982). Access to vegetative cover, log cover, and burrows may be further impacted by the concentration of deer mice and other rodent species (Van Horne 1982a, Sharpe and Millar 1991).

There are two other forms of deer mouse "predation" that can occur, conspecific aggression and pathogenic, as from disease or parasitism. Aggression in adult male deer mice during the breeding season can cause mortality (or emigration) of juvenile deer mice (Sadlier 1965, Wolff 1989). Intensity of this effect may be density-dependent (Christian 1971). I did not conduct a thorough search for influences by disease and parasites. However, the few studies encountered indicated that parasitism may have little influence on demographic rates, and hence, abundance (Whitaker 1968, Hunter et al. 1972, Sadlier 1974).

Extreme cold temperature is a malentity for deer mice. Cold temperatures in early fall may truncate breeding. Further, prolonged cold winter temperatures require additional energy for heat production, increase water demand, and lower future survival and reproduction when food is limited (Selander 1951, Merritt and Merritt 1980, Porter and McClure 1984). In contrast, given adequate energy reserves or available food and water, warm fall temperatures may extend the normal breeding period (Wunder and Byman 1979) and warm spring temperatures can stimulate early breeding (Sadlier 1974, Millar 1984, Myers et al. 1985). The impact of cold temperatures may be mediated by use of high quality nests, snow cover, or huddling behavior (Howard 1951, Stebbins 1977, Porter and McClure 1984, Wolf 1989, Sharpe and Millar 1991). Large concentrations of deer mice may prove either deleterious, forcing some individuals to use low quality nest sites, or beneficial, by forcing groups to use the same burrow.

The conceptual pathways described in the envirogram of deer mouse abundance suggest a global model with far too many parameters to estimate reliably given the amount and types of data collected during this study. I therefore chose to limit global models to nine parameters and candidate models to a maximum of eight parameters for the purpose of identifying dominant effects. An eight-parameter model would include an intercept, six coefficients for ecological effects, and an estimate of a proper variance term. I anticipated a minimum ratio of sample size (i.e., number of site-year estimates of biomass) to estimated parameters of approximately 5:1. This ratio is small and I therefore used a small-sample correction when estimating the model-selection criterion (AIC_c as described below; Burnham and Anderson 1998).

Given the documented ecological relationships (Fig. 2.3), imposed limits on parameters, and types of data collected during this study I proposed and estimated parameters in nine *a priori* and seven additional (exploratory) models that predicted abundance of deer mice (Table 2.3). For a global model (DM_{Global}), I proposed that deer mouse abundance (g/ha) was positively affected by the density of mature conifer trees (MCONIF; stems/ha), cumulative rainfall (cm) during spring and summer months (April through August) of two preceding years (PREVRAIN), mean maximum grass and forb height in the same summer (GFHT; cm), number of sexually mature female deer mice in the summer population (MATFEM), and density of cover (COVER) as indexed by total number of shrubs, saplings, and logs (10 cm to 30 cm diameter) per ha. For the global model, I also proposed that deer mouse abundance was negatively influenced by excessive cold temperatures during the preceding fall and winter months (November through February; FWTEMP; °C) and by interference competition by brush mice or voles

(INFCOMP), indexed as the total density ($\hat{N}$/ha) of these species during the same summer. Thus, the DM_{Global} model portrayed the effects of summer and fall food supply (GFHT, MCONIF, PREVRAIN), availability of females during the breeding season (MATFEM), cover from predation during the breeding season (GFHT, COVER), energetic cost during the overwinter period (FWTEMP), and interspecific interference competition (INFCOMP).

Each candidate model (C1–C8; Table 2.3) comprised a logical subset of DM_{Global} or included a surrogate effect. For example, in model C2 and C5, I examined the potential influence of delayed density dependence (DENDEP), as indexed by the density of deer mice ($\hat{N}$/ha) during a preceding summer, in place of interspecific competition (Table 2.3). In models C4 and C5, I also examined the potential effect of alternative prey for some predators (ALTPREY) as measured by biomass (g/ha) of brush mice, both vole species, and Mexican woodrats occurring during the same summer.

I formed seven exploratory models (E1–E7; Table 2.3) after reviewing the results generated for the original nine models and then combining subsets of relatively more important effects (see Model selection below). In model E6 (Table 2.3), I substituted rainfall (cm; RSPRAIN) accumulated during the spring (March–May) preceding the summer that deer mouse abundance as an indirect measure of GFHT. Comparison of results from models E6 with other models would indicate how well an indirect factor like spring rainfall versus a more direct factor like grass-forb production would predict deer mouse abundance. The general purpose of exploratory models was to determine if a more parsimonious model could be formed for future use. However, the most reliable inferences regarding effects of deer mouse abundance should be restricted to parameter

estimation and selection among *a priori* models (Burnham and Anderson 1998).

Brush mouse—information describing ecology of the brush mouse is limited compared to that for the deer mouse. Consequently, the resulting envirogram (Fig. 2.4) is less complex. Similar to the deer mouse, two resources (food and water), mates, predators, and a single malentity (temperature extremes) are presumed to influence summer abundance of brush mice directly. However, the character of food resources, protection from predators or the thermal environment, and potential competitors may differ.

Diets of brush mice vary seasonally, likely with availability of food resources. Common foods include arthropods (butterfly, moth, and beetle larvae; spiders; true bugs [Hemiptera]; camel crickets [*Centhophilus* sp.]), acorns, conifer seeds, juniper berries, fruits from various shrubs, and seeds of grasses or forbs (Bailey 1905, Jameson 1952, Brown 1964a, Duran 1973, Holbrook 1978, Smartt 1978, Goodwin and Hungerford 1979). Acorns, conifer seeds, arthropods, and juniper berries or shrub fruits appear to be important foods during fall and overwinter periods (Jameson 1952). Evergreen leaves and fungi may be consumed in great quantities when other foods are unavailable during this time. Fewer seeds, but more sprouts, are consumed during the spring period, as are more arthropods and leaves of select forbs (Jameson 1952). During summer periods arthropods, flowers, seed heads and fruits are consumed in greater frequency (Jameson 1952, Brown 1964a, Duran 1973, Smartt 1978).

Similar to deer mouse populations, summer abundance of brush mice should, in part, be affected by demographic responses to food and water supply (Fig. 2.4). Extended reproduction in fall months is attributed to ample late-summer or fall crops of acorns,

conifers seeds and/or fruits (Jameson 1953). Survival of brush mice during cold periods also requires adequate food supply (Howard 1951). When the availability of food is reduced, survival can be enhanced by well insulated nests, and huddling (Howard 1951, Wolff 1989). Water, which is probably acquired partially from food (MacMillen 1983) and sometimes from direct sources (*personal observation*), is presumed to affect reproduction in similar ways as that described for the deer mouse. That is, limited water inhibits reproduction and decreases survival of young prior to weaning (Porter and Busch 1978, Nelson and Desjardins 1987). Thus, increased abundance for a particular summer may be triggered, in part, by foods produced in the preceding fall and availability of water in spring foods or free sources at the onset of reproduction. Factors influencing abundance of food for the brush mouse are similar to those described for the deer mouse.

Indirect influences on food and water resources of brush mice (Fig. 2.4) are also similar to those described for the deer mouse envirogram. An exception is that density-dependent influences have not been documented in brush mouse populations. Competition among non-breeding brush mice may not be an important factor, as individual brush mice of either sex show little aggression towards each other (Brown 1964a). However, based on work on other white-footed mice (Wolff 1989), it is presumed here that female mice raising young may inflict aggression towards other, non-related conspecifics, effectively depriving them use of food and water resources. When food and water are limited, this form of territorial defense might limit population increase.

For the same reasons described for the deer mouse, I assume here that brush mouse population dynamics are partly influenced by the availability of mature females

(Fig. 2.4). In addition to habitat quality, the number of mature, female brush mice is likely influenced by social factors. When suitable resources are limited, young females may be suppressed from maturing and reproducing by interactions with territorial (breeding) females (Kaufman and Kaufman 1989). Suppression of maturation may contribute to diminished reproduction in populations of *Peromyscus* spp. (Christain 1971). Ultimately, lack of reproduction may exert a greater impact on numerical decline in brush mouse populations than overwinter mortality (Brown 1964b).

Brush mice likely use dense shrubs, rocks, and dead trees for thermal and anti-predatory cover (Fig. 2.4). These mice typically nest in rock crevices, hollow trees, and logs (Bailey 1905). As described above, oaks, various shrubs, pinyon, and juniper trees produce food for this mouse and its distribution is strongly associated with sites characterized by dense shrubs, particularly oaks, and rocky substrates (Jameson 1953, Hoffmeister and Goodpaster 1954, Brown 1964a, Wilson 1968, Kilpatrick 1971, Holbrook 1978, Armstrong 1979, Goodwin and Hungerford 1979, Cornley et al. 1981, Svoboda et al. 1988, Fellers 1994, Sureda and Morrison 1998). Most importantly, brush mice are known to avoid previously used areas when trees and shrubs are removed (Holbrook 1979b). Disturbance and succession may influence brush mouse cover in multiple ways. For example, fire can remove cover temporarily without altering community composition, stimulate sprouting in some trees or shrubs, or when fire intensity is great, conifer-dominated stands may return as oak-brush fields.

Predators of, and interspecific interactions with, brush mice (Fig. 2.4) differ somewhat from those of deer mice. Only those predators of deer mice that occur in xeric forests can be considered predators of brush mice. Formal study or observations show

that Mexican spotted owls, some diurnal hawks, and some snake species take brush mice (see Chapter 3, Brown 1964b). It is assumed here that co-occurring mammalian predators (e.g., bobcats; coyotes) also kill brush mice. Competition with other species may also impose little influence. For example, in central Arizona, brush mice were not influenced by removal of deer mice and at least one woodrat species (Stephens' woodrat [*N. stephensi*]) (Holbrook 1979a; b). However, habitat requirements of Mexican woodrats appear more similar to those of brush mice than are those of Stephens' woodrat (Findley et al. 1975, Goodwin and Hungerford 1979). Further, Mexican woodrats are weak stick-nest builders, often nesting in logs, tree cavities, or rock dens (Finley 1990; *personal observation*). Thus, Mexican woodrats and brush mice may compete for nest sites. Finally, as is proposed for deer mice, predation pressure on brush mouse populations may be relieved when other prey are abundant.

Given the ecological relationships documented for brush mice (Fig. 2.4), I proposed and estimated parameters in 14 *a priori* and eight additional (exploratory) models that predict summer abundance of these mice from multiple potential factors (Table 2.4). For a global model (BM_{Global}), I proposed that brush mouse abundance (g/ha) was positively affected by the density of pinyon and juniper trees (PJTREE; stems/ha), cumulative rainfall (cm) during spring and summer months (April through August) of two preceding years (PREVRAIN), density of all shrubs (SHRUBS; stems/ha), amount of rock cover (ROCKS; %) and the abundance of alternative prey for some predators (ALTPREY) as measured by biomass (g/ha) of deer mice, both vole species, and Mexican woodrats during the preceding breeding season. For the global model, I also proposed that brush mouse abundance was negatively influenced by excessive cold temperatures

during the preceding fall and winter months (November through February; FWTEMP; °C) and interference competition by Mexican woodrats (INFCOMP), as indexed by their density ($\hat{N}$/ha) during the same summer. Thus, the BM_{Global} model portrayed the effects of summer and fall food supply (PJTREE, PREVRAIN, SHRUBS), cover from predation during the breeding season (SHRUBS, ROCKS), release from predation (ALTPREY), energetic cost during the overwinter period (FWTEMP), and interspecific interference competition (INFCOMP).

Each candidate model (Table 2.4; C1–C13) either comprised a strict subset of effects proposed in the global model or a subset with one or two different parameters substituted for the original, global effects. For instance, in candidate models C2, C4, C6, C8, C9, and C11, density of oaks, both stunted and tree-sized (OAKS; stems/ha), was substituted for SHRUBS as a food-related effect. Comparison of similar models including SHRUBS with those including OAKS would be useful in determining whether a general (from all shrubs) mast source or a specific source (from oaks) had a greater influence on brush mouse abundance. Other substituted parameters that might have a positive influence on brush mouse abundance included grass and forb production (GFHT) in the same summer that brush mouse abundance was measured, density of logs (>10 cm diameter) and dead trees (LSCOV) as nest site and cover sources, and cumulative rainfall during the preceding spring (RSPRAIN; cm) as an index of available water.

I formed eight exploratory models (E1–E8; Table 2.4) after examining the results generated for the original 14 models and I included subsets of effects common to the most likely models. These models represented a reduced parameter set that portrayed different combinations of effects by food supply, availability of mates, and quantity of rock cover.

Mexican vole—Information detailing the ecology and population biology of Mexican voles is very limited. To construct an envirogram for this species (Fig. 2.5), I relied primarily on information pertaining to the ecology of meadow voles (*M. pennsylvanicus*). I focused on the meadow vole because of apparent evolutionary and ecological similarities with the Mexican vole. Based on distribution patterns and the fossil record, Mexican voles are believed to be derived from a meadow- vole lineage (Hoffman and Koeppl 1985). Karoytypes are very similar between these two species (Gaines 1985), some aspects of reproduction are comparable (Hilton 1992), and both species occupy isolated, relatively small patches of grass-dominated habitats (Getz 1985). Mexican voles do differ with respect to maximum litter size, which is a third (4 versus 12) of that reported for the meadow vole (Keller 1985). Also, the former species can tolerate more arid environments (Getz 1985, Hoffman and Koeppl 1985). Whether these different traits lead to differences in population dynamics is unknown. I therefore integrate information specific to the Mexican vole when available.

Food and water are primary resources believed to affect abundance of Mexican voles (Fig. 2.5). There is a stark absence of information describing specific food habits and effects food selection may have on demography of this species. Most members of the genus *Microtus* consume monocotyledon or herbaceous dicotyledon plants (Batzli 1985). This generalization has been applied to Mexican voles following observations of plant cuttings found in runways (Spicer et al 1985) and analysis of stomach contents from 10 individuals (Hilton 1992).

Meadow voles consume primarily vegetative parts of a select number of plants. Reported genera include *Poa*, *Muhlenbergia*, *Festuca, Trifolium*, *Vicia*, *Ambrosia*,

Taraxacum, *Achillea*, *Bromus, Phleum*, and *Panicum* (Zimmerman 1965, Lindroth and Batzli 1984, Bergeron and Jodoin 1994). However, consumption of different plant types or parts may vary according to season. More monocots may be consumed during winter and spring whereas more dicots may be consumed during summer and fall (Lindroth and Batzli 1984). *Poa pratensis* may be consumed in greater amounts and *Vicia cracca* in lesser amounts during winter (Bergeron and Jodoin 1994). Also, conifer seedlings or bark may be consumed during winters when herbaceous plants are unavailable (Bucyanayandi et al. 1992). Leaves and new stems are consumed during spring and summer, older stems during late summer and fall, and desiccated stems and leaves during winter (Bergeron and Jodoin 1993). Seed heads and plant roots are consumed in small amounts during all seasons but more so during fall and winter (Gates and Gates 1980, Lindroth and Batzli 1984). Other foods consumed in appreciable amounts include fungi (up to 21% by volume) taken during spring or fall, and arthropods (Coleoptera, Lepidoptera, Orthoptera; up to 36% by volume) which may be consumed year round (Zimmerman 1965, Lindroth and Batzli 1984, Fish 1974).

Many vole species are restricted to mesic or wet grasslands, in part because of inefficient renal processes (Getz 1963; 1985). Voles obtain water through their food or from dew (Getz 1985). During dry periods, dehydration may inhibit reproduction or survival of young and meadow vole populations may decline despite abundant food (Mihok 1984, Keller 1985, Ostfeld and Canham 1995). Although Mexican voles are apparently adapted to more arid environments, it is assumed here that this species also obtains water from its food and population declines may ensue following prolonged periods of drought that cause plant desiccation and vole dehydration.

Both food availability and quality affect vole abundance (Fig. 2.5). The quantity of different food plants consumed by meadow voles usually corresponds with plant abundance (Zimmerman 1965, Bergeron and Jodoin 1987) and in some cases caloric content (Gates and Gates 1980). However, a few plants (*Trifolium pratense*, *Festuca rubra*, and *Vicia cracca*) may be preferred over others. Seasonal use of commonly consumed plants, plant parts, or selective use of preferred plants often corresponds to greater digestibility (i.e., plants with lower amounts of phenolics, tanins, and fiber, and with greater amounts of protein, non-structural carbohydrates, and water; Lindroth and Batzli 1984, Bergeron and Jodoin 1987; 1994, Bucyanayandi et al. 1992). When plants with greater digestibility are readily available, more voles may endure winter in better condition, grow to sexual maturity sooner, and breed early (Lindroth and Batzli 1984). Mexican voles will breed during winter months when vegetation is not covered by snow (Hilton 1982). Similarly, when new plant growth becomes available in spring following deep snows, these voles will also reproduce (Hilton1982). Young (spring) plants contain relatively more protein and water, and less fiber (Goldberg et al. 1980, Bergeron and Jodoin 1987) than older plants. New growth may also contain a chemical compound (6-methoxybenzoxazolinone) that triggers reproduction in voles (Sanders et al. 1981, Berger et al. 1981). As plants age, levels of some phenols (e.g., cinnamic acids) that inhibit vole reproduction may increase (Berger et al. 1977). Consequently, availability of high quality forage through its affect on early and prolonged reproduction is considered a primary factor for large increases in vole numbers (Lindroth and Batzli 1984, Batzli 1985, Taitt and Krebs 1985, Bergeron and Jodoin 1987).

I suspect similar relationships may apply to Mexican voles in the Sacramento

Mountains because ecological conditions of occupied montane meadows parallel those described for meadow voles occupying old-fields. In both cases, these voles are occupying patches of grassland that have succeeded from lands disturbed by agriculture (Kaufmann et al. 1998). Many of the plant genera consumed by meadow voles occupying old-fields (listed above) can be found in the montane meadows occupied by Mexican voles of this study (see Appendix 1.A). In particular, *Poa pratensis*, a very common food plant of meadow voles, is a dominant species in the montane meadows of the Sacramento Mountains.

Availability of quality forage to Mexican voles will be influenced by environmental factors that affect plant production, grazing, and abiotic disturbances (Fig. 2.5). Plant production is enhanced by warm temperatures during the early part of the growing season and adequate soil moisture (Vaughn 1974, Harper 1977, Walker et al. 1994). The latter will be influenced by winter snow packs, spring precipitation, and soil properties. Plant production during a given growing season will also depend in part on production and conditions during the preceding growing season, which affect the amount of nutrients stored and available for future production (Harper 1977). Composition of available forage will vary according to plant community type and local site conditions. Forage biomass can be reduced by a number of abiotic or biotic disturbances including fire, land development, and grazing (Fig. 2.5). Effects on vole forage and ultimately vole abundance will vary according to extent and intensity of each disturbance. Effects of grazing on grasslands are better known (e.g., see Milchunas 1993) and likely to be the most current form of meadow disturbance in the study area. Grazing by domestic livestock or native herbivores may reduce vole abundance when great amounts of food

plants are removed and excessive use and associated damage (e.g., compaction or trampling) stifles future production of the vole's food plants (Birney et al. 1976). Voles also reduce their own food supply. High densities of meadow voles can effectively remove significant portions (32–76%) of biomass of high quality foods during the growing season (Bergeron and Jodoin 1989, Bucyanyandi 1991). This extent of exploitation during a summer can significantly reduce the quantity of resources (52%) available to these voles in the following spring (Bergeron and Jodoin 1993). Such impacts imply a density-dependent mechanism for meadow vole populations. Here, it is assumed that Mexican voles might also remove needed forage at high densities (Fig 2.5). In contrast, light to moderate disturbance may stimulate new growth and improve forage quality or stimulate chemical changes in some plant species that ultimately promote vole reproduction (Sanders et al. 1981).

The availability of females capable of breeding may have a strong influence on summer abundance of Mexican voles (Fig. 2.5). No more than four young are produced per litter in this species and the mean is approximately 2.3 young/litter (Brown, L. 1968, Choate and Jones 1970, Keller 1985, Hilton 1992). Given the low litter size, high summer densities may only be possible when a large number of females produce multiple litters. This may require that breeding begin early and that subadult females mature rapidly. Thus, the number of mature females in the population at the onset of breeding is likely an important factor for population increase in this species (Hoffmann 1958, Christian 1971, Conley 1976).

Aside from availability of quality forage, intra- and interspecific interactions can influence the availability of sexually mature female voles (Fig 2.5). Here I assume that

the mating system, social and spacing behavior of Mexican voles is similar to that of meadow voles. The latter species is promiscuous or polygamous, whereby females establish and defend territories for raising young and males compete for breeding opportunities rather than physical space or resources (Madison 1985, Wolff 1985b, Boonstra et al. 1987, Ims 1987). Sexual maturity of subadult female voles may be delayed in the presence of one or more adult females, particularly over winter periods when limited resources may slow development and when grouping behavior (e.g., huddling) can enhance an individual's survival (Webster and Brooks 1981, Madison 1985, Wolff 1985b). During breeding periods, aggression associated with territoriality of mature females may require that subadults disperse before they can acquire the resources to mature and reproduce (Getz 1961, Madison 1980, Lidicker 1985, Ostfeld and Canham 1995). When spacing among individual meadow voles or territorial boundaries are diminished during high densities, maturity of subadult females is inhibited and breeding can diminish or cease (Christain 1971). Successful dispersion of subadults will also depend on suitable cover (Peles and Barrett 1996). Thus, a maximum number of females available for breeding may occur when spacing dynamics and resources permit many, small territories in a given area (Taitt and Krebs 1985).

Distribution of female Mexican voles may be concentrated further by the presence of long-tailed voles (Fig 2.5). The latter species is behaviorally dominant and high densities may effectively create a dispersal "fence" for Mexican voles (Conley 1976, Lidicker 1985). Under such situations, long-tailed voles may indirectly trigger high densities of Mexican voles. Containment by long-tailed voles may also foster intraspecific aggression among Mexican voles (Conley 1976). If so, the distribution of

long-tailed voles could affect indirectly the availability of Mexican vole mates.

Predators affect abundance of Mexican voles by removing individuals or possibly by restricting habitat use (Fig. 2.5). All of the predators known to take deer mice (see above), likely consume Mexican voles (USDI 1991). Certain snakes (garter snakes [*Thamnophis* spp.]; gopher snake) may take voles more commonly than other prey (Johnson and Johnson 1982). The effect of predation can be considerable, particularly when numerous predators are attracted to high densities of voles and predator occupancy is prolonged by their use of other prey (Pearson 1985). Subsequent population growth can be delayed under these circumstances, despite the availability of food. However, when voles are alternative prey for a predator, abundance of other prey species (e.g., deer mice or long-tailed voles) may provide release from predation (Fig 2.5). The latter scenario may apply to predation by spotted owls (see Chapter 3).

Ample herbaceous or snow cover is a primary deterrent to predation of voles (Fig 2.5). Significant numbers of meadow voles may be removed by predators following reduction of vegetative cover (Getz 1970, Baker and Brooks 1981; 1982). Apparently, there is a threshold level of herbaceous cover that must be exceeded before rapid increases in meadow vole numbers can occur (Birney et al. 1976). Also, both density and survival of adult meadow voles increase (asymptotically) with abundance of herbaceous cover (Adler and Wilson 1989). Although the abundance of herbaceous vegetation provides food, it is protection from predation and the thermal environment that is considered the stronger effect (Peles and Barrett 1996). When snow covers dense vegetation, a subnivean environment is created that provides additional protection from predation, thermal cover, and access to food. This combination of factors may foster

future increases in vole populations (Getz 1985, Rose and Birney 1985). The refugia provided by snow cover and its influence on predation are considered primary factors in multiannual fluctuations of microtines in northern Fennoscandia (Hansson and Henttonen 1985). Here it is assumed that adequate cover affects Mexican voles in similar ways and that effects of vole density on its own food supply will also affect condition of its cover resources (Fig 2.5).

Parasitic or pathogenic influences on Mexican vole abundance are unknown. Representatives of four families of mites (Acari), two species of sucking lice (Anoplura), and six genera of fleas (Siphonaptera) have been found on Mexican voles (Timm 1985). Endoparasites of Mexican voles include three species of cestodes and two cecal nematodes (Timm 1985; Frey and Patrick 1995). The effect of parasites on vole demography or abundance are poorly understood (Timm 1985). Mihok et al. (1985) proposed that immunological dysfunction and pathogenic microparasites may play a role in meadow vole declines. However, this interaction is not proposed here as an effect on Mexican vole abundance.

Three malentities, subfreezing temperatures, hot temperatures (>34 °C), and flooding may act to reduce vole abundance. Subfreezing temperatures may increase energy demand, slow growth, and inhibit reproduction in Mexican voles (Wunder 1985, Hilton 1992). Extremely cold temperatures may result in dispersal or mortality of meadow voles, effectively reducing density (Boonstra and Rodd 1983). Meadow voles may mediate the influence of cold temperatures during the nonbreeding season by seeking ground burrows, dense cover, woodland habitat types, and/or huddling (Turner et al. 1975, Madison 1984; 1985). It is assumed here that Mexican voles behave similarly.

Excessive hot temperatures may result in mortality or inhibition of reproduction (through heat stress or dehydration) in meadow voles (Mihok 1984, Rose and Birney 1985, Wunder 1985, Ostfeld and Canham 1995). However, maximum temperatures do not exceed 34°C in the Sacramento Mountains thus it is unlikely that extreme hot temperatures has an affect on Mexican voles in this locality. Periodic flooding following winters with well developed snow packs or during prolonged rain storms is possible in this mountain range. Flooding may lead to temporary losses due to emigration or death (Tamarin et al. 1984).

From the ecological relationships documented for Mexican voles (Fig. 2.5), I proposed and estimated parameters in 11 *a priori* and five additional (exploratory) models that predict summer abundance of these voles from multiple potential factors (Table 2.5). For a global model (MV_{Global}), I proposed that Mexican vole abundance (g/ha) was positively associated with maximum height of grasses and forbs (GFHT), amount of rain accumulated during the preceding spring (Mar–May; RSPRAIN), the number of sexually mature (i.e., lactating or pregnant) females (MATFEM), high densities of long-tailed voles ($\hat{N}$/ha) during the same summer (INFCOMP), and abundance of alternative prey for some predators (ALTPREY) as measured by biomass (g/ha) of both mice species, long-tailed voles and Mexican woodrats during the previous summer. For the global model, I also proposed that Mexican vole abundance was negatively influenced by excessive cold temperatures during the preceding fall and winter months (November through February; FWTEMP; °C) and the density of Mexican voles during the preceding summer (DENDEP). Thus, the MV_{Global} model portrayed the effects of temperature induced energetic demand during the overwinter period (FWTEMP),

summer food supply and cover (GFHT), availability of water or moist conditions (RSPRAIN), availability of female mates (MATFEM), containment by long-tailed voles (INFCOMP), release from predation (ALTPREY), and delayed density dependence (DENDEP).

Each candidate model (Table 2.5; C1–C10) either comprised a strict subset of effects proposed in the global model or a subset with a different parameter substituted for the original, global effect. For instance, in candidate model C9, I substituted total rainfall (cm) accumulated during a previous summer through to the spring (July–May) preceding measurement of Mexican vole abundance (PSSRAIN) as an indirect measure of GFHT.

I formed five exploratory models (E1–E5; Table 2.5) after examining the results generated for the original 11 models. Here, I included subsets of effects common to the most likely models. These models represented a reduced parameter set that portrayed different combinations of effects by summer food and cover, availability of mature females, energetic demand as induced by temperature, and delayed density dependence. I also included a quadratic function of delayed density dependence ($DENDEP^2$) to determine if it provided a better model than a linear function.

Long-tailed vole—Many of the factors that can influence abundance of Mexican voles (Fig. 2.5) likely affect abundance of long-tailed voles (Fig. 2.6). These two vole species are sympatric in montane meadows of the Sacramento Mountains (Conley 1976). However, despite a preference for grassy habitats, long-tailed voles are often found in adjacent shrub or tree-dominated habitats or ecotones (Jenkins 1948, Clark 1973, Findley and Jones 1962, Armstrong 1977, Stinson 1978, Halvorson 1982) either as a means for avoiding other vole species (Colvin 1973, Randall 1978) or to obtain key foods for

surviving fall-winter months (Van Horne 1982b, Spencer 1984). Thus, additional factors concomitant with occupancy of conifer forest-meadow ecotones may affect long-tailed vole abundance in this study area (Fig 2.6).

Long-tailed vole abundance is likely influenced by availability of forbs and production by certain shrub species (Fig. 2.6). For example, when offered 81 different plants (22 trees-shrubs, 42 forbs, 5 sedge-grasses, 5 fungi, 7 other types) long-tailed voles consumed some portion of 72 of these foods (Norrie and Millar 1990). However, only 27 were found to be highly palatable (> 60% consumed). These included 19 forbs, 5 trees-shrubs, and 3 sedge-grasses. According to average palatability scores, forbs were most palatable, followed by sedges or grasses, tree or shrub leaves and fungi (Norrie and Millar 1990). Forbs and young shrub leaves are consumed in spring through early summer, fungi are consumed during late summer through early fall, and fruits or berries of shrubs during late summer through winter (Williams and Finney 1964, Van Horne 1982b, Rhoades 1986). Arthropods (Coleoptera, Diptera, Arachina) may also be taken in low amounts during summer (Van Horne 1982b). When dense snow limits access to forbs, long-tailed voles subsist on bark of shrub stems, saplings, or freshly fallen aspen (*Populus tremloides*) trees or on sedge (*Carex* sp.) (Spencer 1984). Snow covered shrubs may also provide subnivean spaces where existing forbs can be accessed during winter. Survival of adult and juvenile long-tailed voles is believed to be associated with availability of forbs and shrub berries or fruits, respectively (Van Horne 1982b). Low survival may also be associated with low nitrogen content in leaves of shrubs (Van Horne 1982b). It is proposed here, that access to high quality forbs during onset of breeding is also key to successful reproduction by this vole. Like the Mexican vole, long-tailed voles are

believed to obtain water from their food or dew in dense ground vegetation. Accordingly, greater densities of long-tailed voles should be expected in shrub-dominated habitats with ample herbaceous plants (Halvorson 1982, Van Horne 1982b).

A number of abiotic and biotic interactions can affect the amount or availability of this vole's food and water supply (Fig. 2.6). Several of the factors that influence food of the Mexican vole (e.g., previous forb production, grazing, fire, land development; Fig. 2.5) likely influence production of key foods of long-tailed voles. In addition, shrub density or diversity, along with abiotic interactions that influence shrub growth and reproduction (e.g., temperature, rainfall), will affect quantity and quality of shrub-related foods. Other disturbances must also be considered. Clear-cut timber harvest can stimulate short-term shrub and forb production in certain plant communities, followed by a reduction in productivity that falls below that in mature forests (Halvorson 1982, Van Horne 1982b). In addition to grazing, browsing by other wildlife species may effectively diminish the availability of foods for long-tailed voles.

Number of mature females is likely to play a key role in increase of long-tailed vole populations (Fig. 2.6). Litter size of long-tailed voles is greater than Mexican voles, ranging from 2–7 and averaging 4.3 young/litter (Keller 1985, Norrie and Millar 1990). It is not known if these voles breed during winter or beneath snow cover. However, females usually produce no more than two litters in a reproductive season (Van Horne 1982b). Thus, it would seem that density is partly influenced by the numbers of subadult females that survive overwinter and become available for breeding during the following spring.

The number of females available for breeding may be influenced by interaction

with other voles (Fig. 2.6). Little is known about the social structure and mating system of long-tailed voles (Wolff 1985b). Here I will assume that social organization of long-tailed voles is similar to meadow voles; that males compete for breeding opportunities among promiscuous females and the latter defend territories for raising young (Wolff 1985b). Movement and home range patterns of long-tailed voles described by Cranford (1984) support this assumption. I also assume that non-reproductive subadults may be tolerated within proximity of territorial females. Thus, large numbers of females may reproduce when environmental conditions permit narrow spacing between territory holders. Avoidance of Mexican voles may act to concentrate long-tailed voles. High densities of Mexican voles may effectively block dispersal of subadult long-tailed voles. High abundance of both vole species may result in additional aggression that ultimately diminishes the numbers of females that reproduce (Conley 1976).

Long-tailed voles are affected by the same predators that take Mexican voles. However, greater predation may occur from avian or mammalian species that forage along forest-meadow edges, rather than meadow interiors, and less by meadow-dwelling snakes (Johnson and Johnson 1982, Van Horne 1982b). The density of shrubs, logs, and herbaceous cover provide protection from predation and the thermal environment (Van Horne 1982b, Cranford 1984). Availability of cover is, in turn, influenced by plant production, succession, and disturbance (Fig 2.6). Density of trees can also influence cover for long-tailed voles. Dense forest stands with closed tree canopy possess less cover for this vole whereas formerly dense stands that have a patchy canopy and accumulated downed logs may provide suitable cover (Halvorson 1982, Van Horne 1982b). Abundance of other prey species, like Mexican voles, deer mice, or woodrats

may afford release from predation by generalist predators.

Parasites are viewed as another form of predator in envirograms. Representatives of two families of mites (Acari), four species of ticks (Ixodidae), four species of sucking lice (Anoplura), and 19 genera of fleas (Siphonaptera) have been found on long-tailed voles (Timm 1985). In addition, five species of cestodes and eight species of nematodes have been reported (Timm 1985). However, because little is known about the affects of parasitism on vole population processes (Timm 1985) their influence on long-tailed vole abundance is not modeled here.

Two malentities are presumed here to influence abundance of long-tailed voles (Fig. 2.6). Both are related to temperature extremes. Cold temperatures (<20 °C) can be tolerated but require greater energy expenditure with decreasing temperature (Beck and Anthony 1971). A quality nest will provide energetic savings by decreasing the temperature at which additional energy is required to maintain homeostasis (from 25 to 20 °C). Long-tailed voles are known to seek areas with denser herbaceous cover for overwintering (Cranford 1984). Sedge-clumps and subnivean spaces created by snow over shrubs may also provide suitable insulation from winter temperatures (Spencer 1984). Individuals that cannot find dense herbaceous cover, especially during cold, snow-free periods will likely perish (Cranford 1984). The second malentity is extremely warm temperature (>32 °C). In a laboratory setting, when ambient temperatures exceed 30 °C, long-tailed voles must expend energy to regulate body temperature (Beck and Anthony 1971). These voles apparently have not adapted behaviors to deal with high temperatures and death occurs when ambient temperature exceeds 32 °C in the laboratory (Beck and Anthony 1971). However, this factor is probably more critical in determining

the occurrence of the species, rather than fluctuations in its abundance. Areas that experience prolonged periods of warm temperature are likely void of long-tailed voles.

From the relationships shown in the envirogram for long-tailed voles (Fig. 2.6), I proposed and estimated parameters in 11 *a priori* and seven additional (exploratory) models that predict summer abundance of these voles from multiple potential factors (Table 2.6). For a global model (LV_{Global}), I proposed that long-tailed vole abundance (g/ha) was positively affected by density of shrubs (SHRUBS; number of stems/ha); maximum height of grasses and forbs (GFHT), the number of mature (i.e., lactating or pregnant) females (MATFEM), the density (number/ha) of logs >10 cm diameter (LOGS), high density of Mexican voles ($\hat{N}$/ha) during the same summer (INFCOMP), and abundance of alternative prey for some predators as measured by biomass (g/ha) of deer mice species, Mexican voles, and Mexican woodrats during the previous summer (ALTPREY). For the global model, I also proposed that long-tailed vole abundance was negatively influenced by excessive cold temperatures during the preceding fall and winter months (November through February; FWTEMP; °C) Thus, the LV_{Global} model portrayed the effects of temperature induced energetic demand during the overwinter period (FWTEMP), food, some water sources, and cover (SHRUBS, GFHT, LOGS), availability of female mates (MATFEM), avoidance of a primary competitor (INFCOMP), and release from predation (ALTPREY).

Each candidate model (Table 2.6; C1–C10) either comprised a strict subset of effects proposed in the global model or a subset with a different parameter substituted for the original, global effect. For instance, in models C3 and C4, I substituted density of long-tailed voles during the preceding summer (DENDEP) for INFCOMP to examine the

potential effects of delayed density dependence. In models C4, C9, and C10 I also modeled the effects of shrubs and grass-forb height as a quadratic function because areas with moderate amounts of both plant forms could be optimal for this vole (Table 2.6). In models C1 and C7, I included total rainfall (cm) accumulated during a previous summer through to the spring (July–May) preceding measurement of long-tailed vole abundance (PSSRAIN) as a factor necessary for shrub fruit production in conjunction with (SHRUBS). Finally, in model C10, I substituted amount (cm) of rain accumulated during the preceding spring (Mar–May; RSPRAIN) as an indirect measure of herbaceous plant production.

I formed seven exploratory models (E1–E7; Table 2.6) after examining the results generated for the original 11 models. Here, I included subsets of effects common to the most likely models. These models represented a reduced parameter set that portrayed different combinations of effects by fall-winter temperatures, food and herbaceous cover, availability of mature females, and interference competition.

Mexican woodrat—Little is known about the population ecology of this species. There is limited information about the food habits, den sites, reproductive traits, and habitat associations of the Mexican woodrat. Where specific information is lacking, I draw on pertinent generalizations stemming from studies of other woodrat species to develop an envirogram for the Mexican woodrat (Fig. 2.7).

As with the previous four species, food and water are viewed as vital resources that can affect abundance of Mexican woodrats (Fig. 2.7). This woodrat consumes primarily foliage or soft vegetative parts from a wide variety of plant species. Examination of contents in dens of 51 Mexican woodrats in Colorado revealed that this

species consumed or stored portions of 9 trees, 35 shrubs, 46 forbs, 6 grasses, 1 vine, and 7 cacti (Finley 1958). In northern Arizona, Vaughan (1990) found that the most common plants occurring in middens were brickellia (*Brickellia californica*; 96% frequency), mountain mahogany (*Cercocarpus montanus*; 56%), alligator bark juniper (*Juniperus deppeana*; 44%), pinyon pine (44%), and prickly pear cactus (*Opuntia macrorhiza*; 40%). Other foods consumed less frequently include mushrooms, reproductive parts of higher plants, and adult lepidopterans (Cornely and Baker 1976, *personal observation*). The wide use of many plants suggests that the Mexican woodrat is a dietary generalist (Finley 1958, Vaughan 1990).

Some selection may occur within the wide variety of plants consumed. Most food stuffs are gathered within in 30–50 m of den sites (Finely 1990, Vaughan 1990), and when accounting for frequency of use and plant frequency near dens, some foods do appear to be selected. For example, in Finley's (1958) study, foliage from junipers was selected most often, followed by foliage from Gambel oak, herbaceous forms of *Artemesia*, mountain mahogany, and pinyon pine. Similarly, Mexican woodrats in northern Arizona preferred foliage of alligator-bark juniper, pinyon pine, and brickellia (Vaughan 1990).

Food may be selected to fulfill water requirements. Several species of woodrats, including those dwelling in arid environments, demonstrate a poor ability for concentrating urine and cannot subsist solely on metabolic water (Lee 1963, Cornely 1979). This is particularly true of Mexican woodrats, which concentrate urine poorly and usually perish in captivity without free water or succulent food (Boice 1969, Brownfield and Wunder 1976). Other species of woodrats occurring in xeric environments take a

wide variety of deciduous shrubs during wet seasons but shift to foliage of evergreen plants that maintain higher moisture content during the dry season (Dial 1988). Some woodrat species may also rely on cacti for water (Olsen 1976, Dial 1988). Although Mexican woodrats can digest secondary compounds (oxalate) found in *Opuntia*, they typically avoid consumption of cactus (Finely 1958, Justice 1985, Vaughan 1990). The selection of juniper and pinyon, as described above for Mexican woodrats in Colorado and northern Arizona, may be for their relatively greater water content. Thus, quality foods for the Mexican woodrat (i.e., those that when locally abundant increase reproduction or enhance survival) probably include forbs of the genus *Artemesia* during the spring (Finely 1958), shrubs like mountain mahogany or brickellia during summer months, and conifers like pinyon pine or juniper during drier periods. Mexican woodrats cache food items in middens for use during fall-winter periods (Finley 1958). Most collecting and storing activity occurs during late-summer through fall (Vaughan 1990). Hence, summer and fall food sources may also be important for overwinter survival.

Availability of quality foods will depend upon a variety of environmental interactions (Fig. 2.7). Productivity of key plant species will be influenced by abundance of those species, and soil moisture and temperature. In turn, these factors are influenced by amounts of solar radiation, ambient temperatures, previous rainfall and snow pack, type of plant community existing in a particular area, and disturbance events (e.g., fire; logging). In the latter case, disturbances that remove enough overhead canopy to stimulate forb production without removing too much security cover can lead to increased abundance of woodrats (McMurry et al. 1993). In contrast, timber harvest that removes food plants near den sites may have detrimental effects (Castleberry et al. 2001). Because

Mexican woodrats rely on existing structures for dens and because woodrats usually forage proximal to dens (30–50 m; Finely 1990, Vaughan 1990), the location of den sites may also affect indirectly the access to high-quality foods.

It is unknown if Mexican woodrats obtain free water in the wild. It is assumed here that sometimes they do use free water. In such cases, recent rainfall will provide a free source of water in addition to enhancing food quality (Fig. 2.7).

The number and distribution of mature females in a given population will also influence abundance of Mexican woodrats (Fig 2.7). Adult females of this species produce on average 3.0 young/litter (maximum of 4 young/litter) and 2–3 litters per year (Finley 1958, Brown 1969, Cornely and Baker 1986). The breeding season for Mexican woodrats in Colorado extends from March to August (Brown 1969). Breeding may occur over longer periods at southern latitudes (Cornely and Baker 1986). Females born in April or May can produce litters during the same season of their birth but usually with a lower number of young (average 2.4; Brown 1969). Because of this relatively low reproductive potential, high densities will likely occur only when reproductively active females can concentrate in a given area up to the limits that territorial behavior will permit. This condition may occur when suitable dens are available and survival of juvenile females over non-breeding periods is high. Survival of juvenile females may be enhanced if their mothers share den sites and food caches, as has been observed for bushy-tailed (*N. cinerea*) woodrats (Moses and Millar 1994).

Predation may play a key role in limiting population growth of Mexican woodrats. These woodrats have been taken by a number of predators including snakes, hawks, owls, roadrunners (*Geococcyx californianus*), skunks, badger (*Taxidea taxus*), gray fox, ringtail

cat, coyote, and bobcat (Cornely 1979, Cornely and Baker 1986, Finley 1990). In the Sacramento Mountains, Mexican woodrats are the preferred prey of Mexican spotted owls (see Chapter 3). Like all woodrat species, Mexican woodrats avoid predation by concentrating their activities near their dens (Vaughan 1990). Other species of woodrats typically travel through low growing cover, collect food items and return immediately to den sites to consume or store those items (Wiley 1971, Thompson 1982b, Finley 1990). Accordingly, natural dens and houses constructed by woodrats are a primary source of protection from predation (Finley 1958; 1990, Vaughan 1990). Because Mexican woodrats typically do not build stick houses they must rely on abandoned houses constructed by other species (e.g., white-throated woodrats) or natural dens beneath boulders, rock crevices, or cavities in trees and logs (Finley 1958, Cornely and Baker 1986). When such features are scarce, den sites and their afforded protection from predation will be limited. When predators remove all homeless woodrats, they effectively limit the size of woodrat populations to a carrying capacity imposed by the availability of dens. The presence of other alternative species may either provide release from predation, or increase predation risk by maintaining predators in the vicinity.

Security cover around den sites may also limit predation on Mexican woodrats (Fig 2.7). Proximal cover may also be a requisite for selection of den sites (Olsen 1973). Important sources of cover include a dense understory like that created by tree saplings or shrubs, rock piles or overhangs, and large downed logs (Finely 1958, Howe 1978, Cornely and Baker 1986). The amount and quality of cover available will depend on the type of plant community at a particular site. Late seral-stages of mixed-conifer will typically have more large downed woody material (Regan 1997). Xeric plant

communities may have more low growing oaks. Disturbance (e.g., fire; logging; brush removal) and succession influence cover of Mexican woodrats directly or indirectly through influences on plant communities (see examples mentioned above). Without security cover, Mexican woodrats are vulnerable to predation while moving material to dens.

Under the terminology used in envirograms, parasites may pose a second form of predation. Parasites recorded for Mexican woodrats include, three species of ticks (Ixodidae), four species of mites (Laelaptidae, Dermanyssidae), nine species of larval chiggers (Trombiculidae), one species of sucking lice (Haematopinidae), one species of cone-nosed bug (Reduviidae), seven species of fleas (Hystrichopsyllidae, Ceratophyllidae), one tape worm (Taeniida), and bot fly larvae (*Cuterebria* sp.; Finley 1958, Hoffmeister 1971). However, the effects of endo- and ectoparasites on abundance of Mexican woodrats are poorly understood and therefore are not modeled.

Competition may play an important role in den ownership (Fig 2.7). Except for brief periods of the mating season, usually one individual woodrat occupies a den (Finley 1958). Mexican woodrats may occupy stick houses of white-throated woodrats, the only other woodrat species occurring in the study area (Finley 1958). Mexican woodrats are behaviorally dominant over white-throated woodrats and may out compete them for stick houses or dens (Howe 1977; 1978). In other species, dominant individuals within the sexes may obtain higher quality den sites (Vaughan and Schwartz 1980, Moses and Millar 1994). Intraspecific competition and dominance within sexes may also determine den ownership by Mexican woodrats. Further, if densities exceed the number of dens that can be occupied, then den scarcity may provide negative feed back on growing

populations.

Malentities for Mexican woodrats include temperature extremes (hot or cold) and over abundant rainfall . Because these woodrats have a poor ability to conserve water, extended periods of hot temperatures that lead to drought may be detrimental. Likewise, extended periods of cold weather may be energetically draining. Over abundant rainfall may reduce juvenile survival. All of these factors, however, are usually mitigated by selection of a suitable den (Dial 1988). For example, during cold, snowy, and windy nights, Mexican woodrats usually remain in their dens and feed from cached foods (Vaughan 1990). Dens or houses along with overhead vegetation reduce thermoregulatory costs in other species of woodrats (Brown, J. 1968, Olsen 1973). The extent of energy savings will depend on the quality of the den, and as discussed above, this may be determined by social interactions.

From the relationships shown in the envirogram for Mexican woodrats (Fig. 2.7), I proposed and estimated parameters in 12 *a priori* and seven additional (exploratory) models that predict summer abundance of these woodrats from multiple potential factors (Table 2.7). For a global model (MW_{Global}), I proposed that Mexican woodrat abundance (g/ha) was positively affected by density of conifer saplings (CSAPL; number of stems/ha), density of shrubs (SHRUBS), number of mature (i.e., lactating or pregnant) females (MATFEM), amount (%) of rock cover (ROCKS), and density (number/ha) of logs >30 cm diameter (LGLOG). For the global model, I also proposed that Mexican woodrat abundance was negatively influenced by maximum height of grasses (GFHT), and density of Mexican woodrats during the preceding summer (DENDEP). Thus, the MW_{Global} model portrayed the effects of food and water supply (CSAPL, SHRUBS,

GFHT), availability of female mates (MATFEM), cover (SHRUBS, ROCKS, LGLOG), and delayed density-dependence (DENDEP).

Each candidate model (Table 2.7; C1–C11) either comprised a strict subset of effects proposed in the global model or a subset with a different parameter substituted for the original, global effect. For instance, in models C3 and C4, I substituted abundance of alternative prey for some predators as measured by biomass (g/ha) of deer mice, brush mice, Mexican voles, and long-tailed voles during a previous summer (ALTPREY) to examine the potential for release from predation. In models C6 and C7, I substituted amount (cm) of rain accumulated during the preceding spring (Mar–May; RSPRAIN) as an indirect measure of herbaceous plant production and available moisture (Table 2.7). In models C9 and C10, I included mean minimum temperatures of fall and winter (Nov–Feb) months as a surrogate for energy demand during the overwintering period. In models C2, C7, and C10, I substituted density of two specific food plants, mountain mahogany and Gambel oak (MTMGOK) for SHRUBS. Finally, I modeled microhabitat effects in C11.

I formed seven exploratory models (E1–E7; Table 2.7) after examining the results generated for the original 12 models. Here, I included subsets of effects common to the most likely models. These models represented a reduced parameter set that portrayed different combinations of effects by the availability of mature females, and cover provided by rocks and large logs. In one model (E6), I also examined a reduced set of microhabitat effects (SHRUBS and ROCKS; Table 2.7).

Model parameter estimation: I formalized each subset of proposed effects on rodent abundance as a linear regression model. The general form used to model

abundance of each species (*i*) was:

$$B_i = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 \ldots \beta_p X_p + \in \quad (2.7).$$

The number of regressor variables (*p*) varied with each candidate or exploratory model, as described above (Tables 2.3–2.7), and $\in$ is the error, or amount of variation in rodent abundance not explained by the proposed effects. I used the method of least squares to estimate model coefficients ($\hat{\beta}_i$). These are maximum likelihood estimates when the assumption of normality holds true.

Structure in this type of model implies that all proposed effects are linear and additive. Ecological trends, particularly generated from long-term data sets, are often found to be non-linear and multiplicative rather than additive (Brown and Rothery 1993). I chose to use a linear, additive form given the short study period, and as a compromise between having enough data or *a priori* justification to incorporate non-linear effects and producing a parsimonious model. Non-linear forms require estimation of additional parameters. Given the sample of estimates of biomass coupled with microhabitat parameters associated with each site during a given year (n = 42 site-year combinations), only a few effects could be examined as non-linear forms. Instead, I examined a larger set of potential effects using a more simplistic (linear) model form. The utility of multiple linear regression for quantifying effects on animal abundance or wildlife-habitat relationships has been demonstrated elsewhere (Davidson and Andrewartha 1948, Brennan et al. 1986, Morris 1987c, Ives 1995).

There are several other assumptions associated with multiple linear regression including, (1) expected value of $\in_i$ is 0; (2) variance of $\in_i$ is constant; (3) $\in_i$ are normally distributed; (4)) $\in_i$ are independent (Ott 1993:692). Violations of these assumptions

affect inferences about model selection or fit under the traditional paradigm of hypothesis testing (which was not relied upon here) and estimation of parameter variances (still a legitimate concern under the I-T approach). In addition, use of this model form (Eq. 2.7) implies that values for regressor variables are measured without error.

I evaluated and treated the first three assumptions in the following manner. First, if a good model is selected, then the zero expectation among $\in_i$ will likely be met (Ott 1993). I presumed that adhering to the model selection procedures advocated under the I-T approach would lead to the "best" model or set of models given the collected data, and therefore satisfy the assumption of zero expectation. Second, I evaluated homoscadasticity of errors using univariate plots of standardized residuals verses predicted values of $\boldsymbol{B}$ and White's (1980) test of heteroscadasticity (SAS Institute 2000). I transformed dependent variables when a suitable transformation was apparent in order to meet this assumption. Otherwise, I reported any models that violated the assumption of constant variance. Third, I checked normality of $\in_i$ by examining histograms of residuals and normal probability plots. Violations of this assumption would be less influential if the variance of error terms was constant. I transformed variables that deviated significantly from a normal distribution.

Statistical independence of $\in_i$ is an important assumption but unfortunately could not be tested. Rather, I tried to ensure independence through the initial sampling design or *posteriori* subsampling of collected data. Violations of independence of $\in_i$ may result in underestimates of variance for the estimated dependent variable, and hence predictions with low precision. However, the goal of this analysis pertains more to identifying key

ecological regressors for conducting future experiments, rather than making precise forecasts from them.

In general, values input for a regressor variable were estimated from data gathered at a particular trapping grid (site) in a given year. Variables comprising estimates of rodent abundance (e.g., interspecific competition, alternative prey) were based on independent observations. However, site specific samples of microhabitat features varied in size from a given year and in some cases were gathered from a systematic set of trapping stations, rather than a random set. To reduce potential influence on microhabitat regressors caused by unequal non-random samples among years, I first pooled all observations (n = 105 or 121) of those microhabitat components that I reasoned were unlikely to change at a given site during the three-year sampling period (1992–1994; e.g., density of shrubs, large conifers, or logs) and then I selected a random subsample (without replacement) of 33 observations. I used the mean calculated from each subsample as the site-year value input into a model (max = 3 values, one for each year). These subsamples were taken irrespective of the year in which the observations were actually recorded. I did not subsample observations of those microhabitat components likely to change over a three year period (e.g., maximum grass-forb height; percent herbaceous cover). Model inputs for these variables were based on the year that these data were actually collected. Finally, regressor variables depicting weather were statistically dependent in the sense that values for different sites during a given year were estimated using the same predictive equation from site elevation.

Because observations input into the model were actually site-level estimates with associated sampling variation, the assumption of no measurement error was violated.

This form of error was not incorporated into the estimates of variation for each model coefficient. Rather, I assumed that sampling was ample enough at each site to limit sampling variation, which in this case is treated as a form of measurement error. When measurement errors are larger than model residual errors, estimates of variance of model parameters will be underestimated, and precision of model predictions will be misleading.

Model selection: I used Akaike's corrected criterion (AIC_c) as a means for selecting among models. Specifically, I used AIC_c to rank each model and to calculate a weight for gauging relative importance of abundance factors and estimating unconditional variances of regression coefficients. I calculated AIC_c with output from regression results following Burnham and Anderson (1998:48), as:

$$AIC_c = n \cdot \ell n(\hat{\sigma}^2) + 2K + \frac{2K(K+1)}{(n-K-1)} \qquad (2.8).$$

Here, $\hat{\sigma}^2$ is the residual sums of squares divided by n, and K is the number of estimated parameters including an intercept and $\hat{\sigma}^2$. I reported the change in AIC_c ($\Delta AIC_c = AIC_c - \min AIC_c$) for each model as a relative measure of difference among models. I calculated an Akaike weight (Aw_j) for each model j following Burnham and Anderson (1998:124) as:

$$Aw_j = \frac{\exp(-\tfrac{1}{2}\Delta_j)}{\sum_{r=1}^{R} \exp(-\tfrac{1}{2}\Delta_r)} \qquad (2.9),$$

where the summation in the denominator is across all models R and Δ is the abbreviated symbol for change in AIC_c. These weights portray the probability that a particular model is "best" given the set of models examined and data collected. I reported a 95% confidence set as those models ranked according to ascending ΔAIC_c with a sum of $Aw_j \geq 0.95$. The best model would be expected within this confidence set, 95% of the time.

In multiple regression, estimates of model coefficients can vary according to variation within data observations and the composition of regressors (i.e., structure) in the model. In addition, structure of the "best" model may vary with analysis of different samples of data, a condition referred to as model uncertainty. I incorporated these types of variability in estimating model coefficients by estimating mean coefficients (weighted across models) and unconditional variances associated with the model-averaged parameters (Burnham and Anderson 1998:133–135). The mean coefficient for a given regressor variable ($\bar{\beta}_i$) averaged over all models that included $\hat{\beta}_i$ was estimated as:

$$\hat{\bar{\beta}}_i = \sum_{j=1}^{R} Aw_j \hat{\beta}_{ij} \qquad (2.10),$$

with an associated unconditional variance:

$$\hat{var}(\hat{\bar{\beta}}_i) = \left[\sum_{j=1}^{R} Aw_j \sqrt{\hat{var}(\hat{\beta}_{ij} \mid M_j) + (\hat{\beta}_{ij} - \hat{\bar{\beta}}_i)^2} \right]^2 \qquad (2.11).$$

In equation 2.11, $\hat{var}(\hat{\beta}_{ij} \mid M_j)$ is the square of the standard error for a particular regressor coefficient estimated for a given model M_j. I expressed unconditional variation as a coefficient of variation of the model-averaged value ($CV\ [\hat{\bar{\beta}}_i]$), estimated as:

$$CV\ [\hat{\bar{\beta}}_i] = \frac{\sqrt{\hat{var}(\hat{\bar{\beta}}_i)}}{\hat{\bar{\beta}}_i} \cdot 100\% \qquad (2.12).$$

Relative importance (RI) of each regressor was quantified as the sum of Akaike's weights across all models that included that regressor. RI could range from 0 to 1.

Because Akaike weights are specific to a model set, I estimated model-averaged coefficients, unconditional CVs, and relative importance of abundance factors for two sets of models, those originally proposed and a combined set of original and exploratory

models. I used SAS (SAS Institute 2000) for all of these computations.

Secondary evaluation: Some temporal effects of abundance may have been deflated in the modeling approach described above because only a limited time series could be examined in conjunction with microhabitat measurements (i.e., only data from 1992–1994). To evaluate this possibility, I quantified correlations and examined bivariate plots between an extended time series (1991–1996) of rodent biomass and precipitation (cm) accumulated over the (1) spring immediately preceding measurement of rodent abundance, (2) preceding summer, and (3) preceding summer through to the immediately preceding spring. I also examined extended time series of late fall-winter temperatures and biomass of each rodent species. I reported significant correlations ($P < 0.05$) as support for other parameters to consider when planning future experiments.

***Ad hoc* relationships:** Parameter inclusion and model structure were justified according to existing biological information published in the scientific literature. Important parameters affecting populations of the five rodents that were specific to the study area may have been precluded if previously unidentified by investigations from other locations or time periods. To assess the possibility that previously unreported, yet potentially key habitat factors were missed using the modeling approached described above, I estimated correlation coefficients and examined bivariate plots of a species' biomass averaged across time at each site and all microhabitat descriptors collected but not included in previous models. To avoid influence on model development, I conducted this analysis after all abundance models were formulated. Significant linear correlations ($P < 0.05$) or bivariate plots that showed an obvious non-linear relationship were identified as other factors that may also be imperative for future experiments.

RESULTS

Sampling effort and hence the amount of data collected varied according to year, season, and site. During the summers (late-June–mid-August) of 1992, 1993, and 1994, 30 environmental attributes were sampled at 2,318 stations within trapping-grids at 20 different sites (Table 2.1). During 1991 through 1996, 186,716 trap-checks resulted in 7,159 marked individuals of deer mice, brush mice, Mexican voles, long-tailed voles, and Mexican woodrats occurring within three general habitats (Appendix 2.C). Most (82%) of this effort was allocated to summer periods when 95% of the individuals of these five species were captured and marked. Sampling outside of summer periods was limited to two sites in each habitat (MF-M, MM, XF) and was conducted during fall (mid-October through mid-November) 1993, winter (mid-January through mid-February) 1994, and spring (mid-April through mid-May) 1994. Seventeen other mammals, including soricids (3 species), leporids (2 species), other rodents (9 species), mustelids (1 species) and mephitids (2 species), were also captured (Appendix 2.C).

Density Estimates

Of the 465 possible combinations of species, sites, habitats, and time periods where live-trapping could have produced capture data, 243 data sets were used to estimate population size and mean maximum distance moved with Program CAPTURE (Appendix 2.D). Estimates of population size were most commonly based on the assumption that capture probabilities ($\hat{p}$) varied among individuals (M_h; range 28% to 45% of the data sets for each species) or that $\hat{p}$ was constant and equal among individuals (M_o; range 17% to 42%) (Fig. 2.8a). None of the other models was used more than 18%

of the time. Model choice was based on the discriminant function ranks of Program CAPTURE for 213 of the 243 data sets (88%). An alternative model was used on the other 30 occasions. Over the six-year period, average values of $\hat{p}$ and number of individuals encountered from all sites were, respectively, 0.27 and 38 for deer mice, 0.30 and 33 for brush mice, 0.11 and 90 for Mexican voles, 0.14 and 36 for long-tailed voles, and 0.35 and 8 for Mexican woodrats. Distribution of $\hat{N}$ relative to $\hat{p}$ varied among trapping occasion and species and was generally less than optimum for estimating unbiased enumeration errors (Fig. 2.8b). Naive density of deer mice ranged 0.25–50.25 individuals/ha, and $\hat{D}$ ranged 0.25–60.91 individuals/ha over 75 sampling occasions where at least one individual was trapped (Fig. 2.9a). Naive density of brush mice ranged 1.25–25.75 individuals /ha, and $\hat{D}$ ranged 0.16–23.19 individuals/ha over 27 occasions (Fig. 2.9b). Naive density of Mexican voles ranged 0.25–122.22 individuals /ha, and $\hat{D}$ ranged 0.25–183.40 individuals/ha over 41 occasions (Fig. 2.9c). Naive density of long-tailed voles ranged 0.25–43.33 individuals /ha, and $\hat{D}$ ranged 0.25–53.57 individuals/ha over 42 occasions (Fig. 2.9d). Finally, naive density of Mexican woodrats ranged 0.25–4.50 individuals /ha, and $\hat{D}$ ranged 0.25–3.28 individuals/ha over 49 occasions (Fig. 2.9e).

On average, effective sampling areas for each species ranged from 63% to 229% larger than the area of trapping grids. The increase in area was a function of movement. Maximum distance moved for each species, averaged over all sites and time periods, was 53 m, 52 m, 19 m, 29 m, and 59 m for deer mice, brush mice, Mexican voles, long-tailed voles, and Mexican woodrats, respectively. However, movements of the mice and voles

varied over time and as a function of their abundance (Appendix 2.E). Greater abundance appeared to restrict movements in populations of both mouse species. Movements in populations of Mexican voles occurring in meadows or xeric forests, (1) increased with small increases in population size ($\hat{N}$), (2) remained constant over moderate population sizes, and (3) decreased slightly within larger populations (Appendix 2.E). In contrast, movements by Mexican voles in mesic forests appeared to decline with increasing population size. Movements in long-tailed vole populations also increased with moderate increases of population size and decreased when population numbers were great. However, the longest distances traveled by long-tailed voles ranged 50–70 m at 30–50 individuals in a population, and these distances were approximately double the distance traveled by Mexican voles (Appendix 2.E). Movements by Mexican woodrats showed little variation (range = 20–100 m) over the limited range of population change (2–18 individuals/population) observed during the six summers (Appendix 2.E).

Distribution and Abundance Patterns

Abundance of these five rodent species varied among the three habitats and two seral stages of mesic forest. During the six summers, deer mice were found in all habitats but were less abundant (per unit of area) in the xeric forest (Table 2.8). Brush mice were never encountered in montane meadows and found rarely in the mesic forest (either seral stage). This mouse species was clearly associated with xeric forests (Table 2.8). Mexican voles were most abundant in montane meadows, and found occasionally in xeric and mesic forests (Table 2.8). Long-tailed voles were abundant in montane meadows and the mesic forest (both seral stages). This vole species was encountered only once in the xeric forest (Table 2.8). Mexican woodrats were found in all three habitats but only

rarely in montane meadows and these encounters were of individuals that normally dwelled in mesic forests. This woodrat species was slightly more abundant in xeric forests than in mesic forests (Table 2.8).

Error in enumerating biomass was a function of the number of individuals captured. In general, coefficients of variation in enumeration error were >100% when only 2–4 individuals were captured (4 cases in Table 2.8). However, when >5 individuals were marked, enumeration errors were more reasonable (CV $\leq$25%).

Per unit of area, the Mexican vole in montane meadows was the most abundant species during the six summers, averaging 1,740 g/ha. The two next most abundant species were the long-tailed vole in montane meadows and the deer mouse in mid-seral mesic forests (373 and 176 g/ha, respectively). Brush mice and Mexican woodrats in xeric forests exhibited lower abundance during the six summers (139 and 133 g/ha, respectively). However, these values must be viewed as simplistic summary statistics subject to great spatial and temporal variation (Figs. 2.10 and 2.11; see below).

Annual patterns of rodent abundance varied considerably among species and habitats (Fig. 2.10). Deer mice exhibited exceptional abundance (783 g/ha) within mid-seral mesic forests during the summer of 1991. Moderate levels of abundance (200–300 g/ha) of this mouse were observed in mid-seral mesic forests and montane meadows in the summers of 1994 and 1996. Brush mice were most abundant in xeric forests (240 g/ha) during the summer of 1992. Mexican voles were most abundant in montane meadows (3,380 g/ha) during the summer of 1992. This species was also moderately abundant in montane meadows during 1994 and 1995 (1,900 g/ha, 2,330 g/ha, respectively). Long-tailed voles were also most abundant in montane meadows (730

g/ha) during the summer of 1992. This vole species was moderately abundant in mid-seral mesic forests (432 g/ha, 516 g/ha) during the summers of 1991 and 1992, respectively, and in late-seral mesic forests (390 g/ha) during the summer of 1996. The greatest observed abundance of Mexican woodrats occurred in late-seral mesic forest during the summer of 1996 (239 g/ha) when this woodrat species was relatively more abundant in all habitats compared to previous years (Fig. 2.10). However, Mexican woodrats occurring in xeric forests were slightly more abundant during most years compared to other habitats. The greatest abundances of this woodrat in xeric forests were observed during 1992 and 1996 (185 g/ha and 211 g/ha, respectively). Overall, annual trends in abundance were not synchronous among these five species.

The seasonal patterns in biomass during one annual period (summer 1993 to summer 1994) also varied among rodent species and habitats (Fig. 2.11). Deer mice were less abundant in montane meadows during the winter of 1994 (10 g/ha) and lowest in mid-seral mesic forests during the fall of 1993 (32 g/ha). Abundance of deer mice in xeric forests exhibited greater consistency during this annual period (range of seasonal means 57–104 g/ha), with the greatest abundance occurring during the fall of 1993. This species exhibited rapid population increase between the spring and summer of 1994 in mid-seral mesic forest and montane meadow habitats while population increase was only moderate in xeric forests (Fig. 2.11). The abundance of brush mice in xeric forests was lowest during the fall of 1993 (60 g/ha). Population increase of this species was only moderate in the xeric forest (Fig. 2.11). Abundance of the other three rodent species was lowest during the spring of 1994, irrespective of habitat type. Mexican voles exhibited a greater population increase between the spring and summer of 1994 than did long-tailed

voles (Fig. 2.11). Mexican woodrats exhibited their greatest abundance during fall of 1993 (156 g/ha) followed by subsequent decreases through the spring of 1994 (Fig. 2.11). This trend was similar for Mexican woodrat populations occurring in xeric forests except that the peak abundance occurred in the summer of 1993 (145 g/ha) rather than the fall (Fig. 2.11). In general, these seasonal fluctuations were more synchronous among species and within habitats compared to annual trends.

Statistical significance of spatial and temporal patterns in summer biomass during 1992–1995 also varied among the five rodents (Table 2.9). Habitat type showed no significant influence on summer biomass of deer mice. Rather, abundance of this species was significantly influenced by factors that varied annually (Table 2.9). Summer biomass of brush mice, Mexican voles, and long-tailed voles were significantly influenced by the interaction of factors related to differences occurring among habitats and years. In contrast, summer biomass of Mexican woodrats was significantly influenced by factors associated with habitat type and only slightly by temporal factors (Table 2.9). There was no significant interactive effect of time and habitat type on the abundance of Mexican woodrats during 1992–1995.

Significant annual variation in rodent abundance was also observed during the summers of 1991–1992 and 1995–1996 (Tables 2.10 and 2.11). Deer mouse abundance declined considerably in mid-seral mesic forests between 1991 and 1992 (Table 2.10) while increasing significantly from 1995 to 1996 (Table 2.11). A significant increase in deer mouse abundance was also observed in the late-seral mesic forest from 1995 to 1996. Brush mouse abundance increased significantly in the xeric forests between 1991 and 1992 (Table 2.10) and again between 1995 and 1996 (Table 2.11). Mexican vole

abundance declined significantly in montane meadows between 1995 and 1996 (Table 2.11), while abundance of long-tailed voles increased significantly in both seral stages of mesic forest during the same period (Table 2.11). The abundance of Mexican woodrats increased significantly in xeric forests between 1991 and 1992 (Table 2.10) and again between 1995 and 1996 (Table 2.11). Mexican woodrat abundance in the late-seral mesic forest also increased significantly between the summers of 1995 and 1996. Thus, the extent of temporal and spatial variation in the abundance of these species described by the balanced data sets gathered during 1992–1995 was conservative.

Biomass of three rodent species also varied between two seral stages of mesic forest but the differences were time dependent. During the summers of 1994 and 1995 abundances of deer mice, long-tailed voles, and Mexican woodrats were statistically equivalent in both mid- and late-seral stages (Table 2.12). However, in the summer of 1996, long-tailed voles were significantly more abundant and Mexican woodrats were nearly so at the late-seral mesic forest site (Table 2.11). Deer mice were generally less abundant in the late-seral stage (Table 2.11).

Abundance Factors

Fifty-seven original and 34 exploratory models were proposed for the five species. The number of parameters estimated for each of these models ranged from three to nine, independent of the species examined. Fit of the five global models (DM_{Global}, BM_{Global}, MV_{Global}, LV_{Global}, MW_{Global}), as measured by the amount of variation in biomass explained by modeled effects (R^2), varied by species and ranged from 61.5% explained variation in deer mouse abundance to 95.5% explained variation in Mexican vole abundance (Tables 2.13, 2.15, 2.17, 2.19, and 2.21).

Six models appeared to violate the assumption of homoscedasticity (MV_{C7}, MV_{E2}, MV_{E3}, MV_{E5}, LV_{C3}, and MW_{E7}). However, only one of these models (MW_{E7}) was weighted heavily in the ranking procedure. Fifty-seven of the models had one standardized residual exceeding the range −3.0 to 3.0. Eleven models had two standardized residuals that exceeded the range, and three models had three values that exceeded the range. Of the 30 models identified as most plausible, the majority (83 %) had one standardized residual that exceeded this range. Plots of standardized residuals from nearly all models showed random patterns. Only one model, $MV_{Global,}$ showed a slight, curvilinear pattern. Overall, the models appeared to satisfy the assumptions of multiple linear regression.

In most cases (4 of 5 species), exploratory models resulted in a more parsimonious model set. The most heavily weighted model describing deer mouse abundance included three regressor variables (Table 2.13). That for brush mice, long-tailed voles, and Mexican woodrats included three, three, and one regressor, respectively (Tables 2.15, 2.19, and 2.21, respectively). The one exception was in models describing Mexican vole abundance. In this case, no exploratory model could provide a more parsimonious model. The global model with seven regressor variables was weighted most heavily according to Akaike's criterion and was therefore considered the most parsimonious (Table 2.17). Exploratory models describing abundance of Mexican woodrats were such an improvement that no original (global or candidate) models were included in the 95% confidence set for all (original plus exploratory) models. For the other species, at least one of the original models was always included in the 95% confidence set for all models.

The structure of plausible models and the relative importance of modeled effects are reported below for each species. Results from both *a priori* (original) and all (original plus exploratory) modeling exercises are presented. Conservative inference should be reserved for results from the original model sets. However, because the primary goal of analysis was to identify key microhabitat components that could be manipulated in future experiments, results from all models are reported.

Deer mouse. Nine original and seven exploratory models predicting summer biomass of deer mice were examined (Table 2.3). Of the nine original models examined, three models (DM_{Global}, DM_{C3}, and DM_{C6}) comprised a 95% confidence set (Table 2.13). Model DM_{Global} was weighted most heavily (0.4822) but not much greater than model DM_{C3} (0.4355). These top three *a priori* models included a total of seven regressor variables (Table 2.14). Two regressors, the density of mature conifers (MCONIF) and the total rainfall during two previous growing seasons (PREVRAIN) were ranked most important (RI = 1), followed by the number of mature female deer mice in the summer population (MATFEM; RI = 0.998), minimum temperature during late fall and winter (FWTEMP; RI = 0.920), and maximum height of grasses or forbs (GFHT; RI = 0.919). Density of shrubs, saplings, and small to medium-sized logs (COVER), and the density of potential competitors during the same summer (INFCOMP) were ranked less important (RI < 0.600). Two other regressors, density of deer mice in a preceding summer (DENDEP) and biomass of other rodents commonly consumed by local predators (ALTPREY) were ranked relatively unimportant (RI = 0).

Coefficients of four of the five top-ranked regressor variables (MCONIF, PREVRAIN, FWTEMP, and GFHT) averaged over the original models were negative

(Table 2.14). Only the model-averaged coefficient associated with MATFEM was positive. However, bivariate plots showed an unclear influence of MCONIF and positive relationships of PREVRAIN and GFHT with deer mouse abundance (Fig. 2.12). The positive relationship of PREVRAIN, MATFEM, and GFHT with deer mouse abundance agreed with relationships predicted in the envirogram. The negative relationship between FWTEMP and deer mouse abundance (Fig. 2.12) was not predicted. Precision of the model-averaged coefficients was highest for MATFEM (CV = 23.3%) and FWTEMP (CV = 41.5%). Precision of coefficients of the other top-ranked regressors was low (>100%; Table 2.14). Thus, when considering relative importance, consistency of quantified associations with predictions, and precision of coefficients among the original models, MATFEM appeared to be the most reliable regressor for predicting summer abundance of deer mice.

In the entire model set, two of the seven exploratory models (DM_{E2} and DM_{E3}) were included along with models DM_{Global} and DM_{C3} in a 95% confidence set (Table 2.13). Model DM_{E2} was weighted most heavily (0.6701) and included three regressor variables (GFHT, FWTEMP, and MATFEM). The 95% confidence set of all models included the same seven regressors reported for the original 95% confidence set. However, relative importance of these regressor variables shifted (Table 2.14). Among all models, MATFEM was ranked most important (RI = 0.997), followed by FWTEMP (RI = 0.954), and GFHT (RI = 0.848). All other regressors were ranked <0.300. Thus, MCONIF and PREVRAIN appeared to be less important in defining a more parsimonious model (Fig. 2.12). In addition, recent spring rainfall (RSPRAIN) was not a strong regressor. Model-averaged coefficients of each regressor also shifted slightly but

direction of the quantified associations remained the same except for GFHT, which shifted from a negative to a positive relationship with biomass of deer mice. Precision of model-averaged coefficients changed slightly, excepting that for GFHT which improved when all models were considered (CV = 113.2% versus 366.9%). Thus, signs of coefficients for MATFEM, FWTEMP, and GFHT averaged over all models were indicative of relationships shown in the bivariate plots (Fig 2.12). Accordingly, these three regressors, with coefficients averaged over all models, provided more reasonable predictions of deer mouse abundance (Fig. 2.12).

Bivariate plots and correlation analyses of extended data sets indicated that recent spring rainfall and large, slightly decomposed logs were positively correlated with summer abundance of deer mice (Fig. 2.12). However, the correlations were relatively weak ($r < 0.50$). The relationship between minimum temperatures during late fall and winter months (FWTEMP) and summer abundance of deer mice maintained significance when data from additional years (1991, 1995, and 1996) were analyzed but the strength of the relationship diminished and approached a quadratic form (Fig. 2.13).

Brush mouse. Fourteen original and eight exploratory models predicting summer biomass of brush mice were examined (Table 2.4). Of the 14 original models examined, two models (BM_{C13} and BM_{C11}) comprised a 95% confidence set (Table 2.15). Model BM_{C13} was weighted most heavily (0.8547). These two *a priori* models included a total of seven regressor variables (Table 2.16). Two regressors, MATFEM and average percentage of rock cover at a site (ROCKS) were ranked most important (RI = 1), followed by density of shrubs (SHRUBS; RI = 0.868). All other regressors were ranked less important (RI < 0.200; Table 2.16).

Coefficients of the three, top-ranked regressors averaged over original models were positive and in concurrence with bivariate relationships (Fig. 2.14) and predictions from the envirogram for this species (Table 2.16). Precision of the model-averaged coefficients was highest for MATFEM (CV = 6.8%). Model-averaged coefficients for ROCKS (CV = 354.6%) and SHRUBS (CV = 11,095.0%) were imprecise. Thus, when considering relative importance, consistency of quantified associations with predictions, and precision of coefficients among the original models, MATFEM appeared to be the most reliable regressor for predicting summer abundance of brush mice.

In the entire set of models, five of eight exploratory models (BM_{E4}, BM_{E7}, BM_{E2}, BM_{E6}, and BM_{E3}) along with one *a priori* model (BM_{C13}) comprised a 95% confidence set (Table 2.15). Model BM_{E4} was weighted most heavily (0.3414) and included three regressor variables, density of oaks (OAKS), MATFEM, and ROCKS. The 95% confidence set of all models included fewer regressors than reported for the original 95% confidence set (Table 2.16). SHRUBS, GFHT, and density of all logs and dead trees (LSCOV) were not included. INFCOMP was added to this 95% confidence set. Relative importance of previously identified regressors shifted except for MATFEM which remained ranked as most important (Table 2.16). Relative importance of ROCKS remained high but decreased in importance compared to original values (RI = 0.710 versus 1). Relative importance of OAKS increased (RI = 0.436 versus 0.105). All other regressors were ranked <0.200. Thus, density of all shrubs (inclusive of low-growing oaks) appeared to be less important than density of oaks (shrub and tree form) in defining a parsimonious model (Fig. 2.14). In addition, recent spring rainfall (RSPRAIN) was not a strong regressor. Model averaged coefficients of each regressor also shifted slightly but

direction of the quantified associations remained the same except for ROCKS, which shifted from a positive to a negative relationship with brush mouse abundance (Table 2.16). This negative coefficient implied a relationship counter to patterns in the data (Fig. 2.14) and predictions in the envirogram. Precision of model-averaged coefficients changed appreciably for one regressor variable. The coefficient for ROCKS was more precise among all models (CV = 299.6% versus 354.6%). Thus, three regressors (MATFEM, ROCKS, OAKS), with coefficients averaged over all models, would likely provide more consistent predictions of brush mouse abundance (Fig. 2.14).

Bivariate plots and correlation analyses of extended data sets indicated that mild temperatures during late fall and winter, percentage of rock cover, and density of conifer saplings were positively correlated with abundance of brush mice (Fig. 2.15). In addition, rainfall during two previous growing seasons and elevation were negatively correlated with abundance of brush mice (Fig. 2.15). Shrub diversity appeared to have a quadratic relationship with abundance of brush mice, whereby high densities of mice were observed at sites with moderately even numbers of shrub species (Fig. 2.15). Relationships between the two weather variables and brush mouse abundance also appeared non-linear in form (Fig. 2.15). Percent rock cover ($r = 0.91$) and elevation ($r = -0.77$) were strongly correlated with brush mouse abundance.

Mexican vole. Eleven original and five exploratory models predicting summer biomass of Mexican voles were examined (Table 2.5). Of the 11 original models examined, two models (MV_{Global} and MV_{C7}) comprised a 95% confidence set (Table 2.17). Model MV_{Global} was weighted most heavily (0.9188). These two *a priori* models included a total of seven regressor variables (Table 2.18). Three regressors, GFHT,

MATFEM, and INFCOMP were ranked most important (RI = 1), followed by RSPRAIN (RI = 0.942), FWTEMP, ALTPREY, and DENDEP (RI = 0.919). Rainfall occurring during a previous summer through to the preceding spring (PSSRAIN) was not ranked as an important regressor (RI = 0).

Coefficients of the three, top-ranked regressor variables (GFHT, MATFEM, and INFCOMP), averaged over original models were positive and in concurrence with bivariate relationships (Fig. 2.16) and predictions from the envirogram for this species (Table 2.18). Model-averaged coefficients of RSPRAIN, ALTPREY, and DENDEP were negative. Direction of the quantified associations with RSPRAIN, ALTPREY, and FWTEMP indicated a relationship counter to that predicted from the envirogram for this species (Table 2.18). Precision of the model-averaged coefficients was high for GFHT (CV = 17.7%), MATFEM (CV = 18.3%), INFCOMP (CV = 20.5%), and DENDEP (CV = 34.0%). Precision of other model-averaged coefficients were less precise (CVs >100%). Thus, when considering relative importance, consistency of quantified associations with predictions, and precision of coefficients among the original models, GFHT, MATFEM, and INFCOMP appeared to be the most reliable regressors for predicting summer abundance of Mexican voles.

Examination of five exploratory models with reduced parameter sets did not lead to a more parsimonious model (Table 2.17). Thus, the 95% confidence set of all models was comprised of the same two *a priori* models (MV_{Global} and MV_{C7}) described above. Relative importance, signs of model-averaged coefficients, and precision measures changed very little between original and entire model sets (Table 2.18). Modeling density-dependence as a quadratic function did not change the relative importance of this

regressor variable. Thus, three regressors (GFHT, MATFEM, INFCOMP), with coefficients averaged over either set of models, provided equally reasonable predictions of Mexican vole abundance (Fig. 2.16).

Bivariate plots and correlation analyses of extended data sets indicated that rain during a previous summer through to the spring preceding measurement of vole abundance ($r = 0.29$; $P = 0.011$; $n = 75$), and percentage of herbaceous cover were positively correlated with Mexican vole abundance (Fig. 2.17). In addition, percentage of shrub cover, percentage of tree cover, percentage of bare ground, volume of small, undecomposed logs, sapling density and diversity, and density of deciduous trees (live and dead) were negatively correlated with Mexican vole abundance (Fig. 2.17). All of these relationships were relatively strong ($r > 0.60$) except for that between Mexican vole abundance and previous rainfall or volume of small logs.

Long-tailed voles. Eleven original and seven exploratory models predicting summer biomass of long-tailed voles were examined (Table 2.6). Of the 11 original models examined, two models (LV_{C2} and LV_{Global}) comprised a 95% confidence set (Table 2.19). Model LV_{C2} was weighted most heavily (0.7187). These two *a priori* models included a total of seven regressor variables (Table 2.20). Five of these regressors, FWTEMP, SHRUBS, GFHT, MATFEM, and INFCOMP were ranked most important (RI = 1). All other regressors were assigned lower ranks (RI < 0.300; Table 2.20).

Coefficients of SHRUBS, MATFEM, and INFCOMP averaged over original models were positive (Table 2.20). Model-averaged coefficients of FWTEMP and GFHT were negative. Relationships with long-tailed vole abundance implied by coefficients for SHRUBS, GFHT, and FWTEMP were counter to bivariate plots of these

data (Fig. 2.18). A plot of SHRUBS with long-tailed vole abundance (Fig. 2.18) showed a negative, nonlinear relationship which was counter to predictions from the envirogram for this species The plot of FWTEMP with long-tailed vole abundance indicated an optimal range of fall-winter temperatures occurring at approximately −7 °C, and the plot of GFHT with long-tailed vole abundance showed a positive relationship (Fig. 2.18). The latter relationship was consistent with predictions in the envirogram. Model-averaged coefficients for MATFEM and INCOMP agreed with bivariate plots (Fig 2.18) and relationships predicted in the envirogram. Precision of the coefficients averaged over original models was highest for MATFEM (CV = 14.9%), INFCOMP (CV = 17.6%), and GFHT (CV = 32.6%). Other coefficients were relatively imprecise (Table 2.20). Thus, when considering relative importance, consistency of quantified associations with predictions, and precision of coefficients among the original models, MATFEM and INFCOMP appeared to be the most reliable regressors for predicting summer abundance of long-tailed voles.

In the entire set of models, two of seven exploratory models (LV_{E4} and LV_{E2}) along with one *a priori* model (LV_{C2}) comprised a 95% confidence set (Table 2.19). Model LV_{E4} was weighted most heavily (0.6063) and included three ecological regressors, MATFEM, INFCOMP, and GFHT. The 95% confidence set of all models included fewer regressors than reported for the original 95% confidence set (Table 2.20). Density of all logs (LOGS) and ALTPREY were not included. Relative importance of previously identified regressors shifted except for MATFEM and INFCOMP which remained ranked as most important (Table 2.20). Relative importance of GFHT remained high but decreased in importance compared to original values (RI = 0.982 versus 1).

Relative importance of FWTEMP and SHRUBS decreased substantially more in rank (RI = 0.381 and 0.093, respectively versus 1). All other regressors were ranked <0.100. Thus, minimum temperatures during late fall and winter, and density of shrubs appeared to be less important in defining a more parsimonious model (Fig 2.18). In addition, quadratic functions of SHRUBS or GFHT did not lead to more parsimonious models (Table 2.19). Model averaged coefficients of each regressor variable also shifted slightly but direction of each quantified association remained the same (Table 2.20). Precision of model-averaged coefficients did not change appreciably (Table 2.20).

Bivariate plots and correlation analyses of extended data sets indicated that rainfall during the previous spring, rainfall during a previous summer through to the spring preceding measurement of vole abundance, rainfall during two previous growing seasons ($r = 0.34$; $P = 0.0003$; $n = 75$), and percentage of herbaceous cover were positively correlated with abundance of long-tailed voles (Fig. 2.19). In addition, percentage of tree cover, percentage of rock cover, percentage of bare ground, and density of deciduous trees (live or dead) were negatively correlated with abundance of long-tailed voles (Fig. 2.19). Only percent herbaceous cover ($r = 0.61$) and density of live deciduous trees ($r = -0.66$) were strongly correlated with summer abundance of long-tailed voles.

Mexican woodrat. Twelve original and seven exploratory models predicting summer biomass of Mexican woodrats were examined (Table 2.7). Of the 12 original models examined, six models (MW_{C5}, MW_{C10}, MW_{C1}, MW_{C4}, MW_{C3}, and MW_{C2}) comprised a 95% confidence set (Table 2.21). Model MW_{C5} was weighted most heavily (0.3597) but not much greater than model MW_{C10} (0.3065). All six *a priori* models included a total of nine regressor variables (Table 2.21). Two regressors, MATFEM and

ROCKS were ranked most important (RI = 1), followed by density of large logs (LGLOG; RI = 0.755), SHRUBS (RI = 0.617) and density of mountain mahogany and low-growing Gambel oak (MTMGOK; RI = 0.383). All other regressors were ranked less important (RI < 0.200; Table 2.22).

Coefficient for MATFEM averaged over original models was positive and in concurrence with bivariate plots and envirogram predictions (Fig. 2.20). Coefficients of ROCKS, LGLOG, and SHRUBS averaged over original models were negative. However, bivariate plots between these variables and abundance of Mexican woodrats indicated that these relationships may have been nonlinear, possibly quadratic in function (Fig. 2.20). Negative relationships for these variables with Mexican woodrat abundance would disagree with envirogram predictions. Precision of model-averaged coefficients was highest for MATFEM (CV = 12.7%). All other model-averaged coefficients were less precise (CVs > 100%; Table 2.22). Thus, when considering relative importance, consistency of quantified associations with predictions, and precision of coefficients among the original models, MATFEM appeared to be the most reliable regressor for predicting summer abundance of Mexican woodrats.

In the entire set of models, all seven exploratory models (MW_{E1}–MW_{E7}) comprised the 95% confidence set (Table 2.21). No original models were included in the 95% confidence set of all models. Model MW_{E7} was weighted most heavily (0.3873), followed by model MW_{E6}. All seven models included four regressor variables, MATFEM, ROCKS, LGLOG, and RSPRAIN. The 95% confidence set of all models included fewer regressors than reported for the original 95% confidence set (Table 2.22). Density of conifer saplings (CSAPL), SHRUBS, GFHT, DENDEP, ALTPREY, and

MTMGOK were not included. Relative importance of previously identified regressors shifted except for MATFEM which remained highly ranked (Table 2.22). Relative importance of ROCKS and LGLOG decreased compared to original values (RI = 0.233 versus 1, and 0.268 versus 0.755, respectively). Relative importance of RSPRAIN increased (RI = 0.277 versus 0). All other regressors were ranked <0.100. Thus, CSAPL, SHRUBS, GFHT, DENDEP, ALTPREY, and MTMGOAK appeared less important in defining a more parsimonious model. Coefficients of most regressors averaged over all models shifted slightly but direction of all relationships remained the same (Table 2.22). The model-averaged coefficient for RSPRAIN increased substantially (Table 2.22). Precision of model-averaged coefficients changed very little compared to those calculated in the original model set. A model with a single regressor (MATFEM) and intercept, parameterized with coefficients averaged among all models, provided a more parsimonious model than one with four regressors (MATFEM, ROCKS, SHRUBS, and LGLOG), parameterized with coefficients averaged among original models (Fig. 2.20).

Bivariate plots and correlation analyses of extended data sets indicated that volume of large, undecomposed logs, diversity of saplings, and density of live deciduous trees were positively correlated with abundance of Mexican woodrats (Fig. 2.21). In addition, percentage of herbaceous cover was negatively correlated with abundance of Mexican woodrats (Fig. 2.21). Percentage of tree cover, percentage of rock cover, large decomposed logs, basal area of live conifer trees, and density of dead deciduous trees appeared to have a quadratic relationship with abundance of Mexican woodrats, whereby high densities of woodrats were observed at sites with moderate amounts of these microhabitat features (Fig. 2.21). All linear correlations with Mexican woodrat

abundance were relatively weak and appeared nonlinear in form (Fig. 2.21).

Seven models (DM_{C7}, BM_{C12}, BM_{E5}, BM_{E8}, MV_{C10}, LV_{C9}, and MW_{C11}) that predicted summer abundance of these rodents entirely from microhabitat descriptors were examined (Tables 2.3–2.7). Relative to other models, these seven models were not parsimonious. Akaike weights for all seven models were <0.0001. Amount of variation in rodent abundance explained by microhabitat descriptors alone was generally low. In only one model (MV_{C10}), did a microhabitat descriptor (GFHT) explain appreciable amounts of variation in abundance of a rodent, in this case, summer abundance of Mexican voles R^2 = 83.7%). Amount of variation explained by the other six microhabitat models ranged from 7.1% to 63.4% but never exceeded 68% of the amount of variation explained by a respective global model (Tables 2.13, 2.15, 2.19, and 2.21).

However, when combined with other biotic or abiotic regressors, at least one microhabitat regressor was ranked relatively important in predicting abundance of each species (Table 2.23). These top-ranked microhabitat descriptors included (1) mean maximum grass-forb height for predicting summer abundance of deer mice, Mexican voles, and long-tailed voles; (2) percent rock cover for predicting summer abundance of brush mice and Mexican woodrats; (3) density of shrubs for predicting summer abundance of brush mice, long-tailed voles, and Mexican woodrats; (4) density of oaks for predicting summer abundance of brush mice; (5) density of large (>30-cm diameter) logs for predicting abundance of Mexican woodrats (Table 2.23).

DISCUSSION

There were two objectives in this chapter, to describe spatial and temporal variation in the abundance of five rodent species commonly consumed by Mexican

spotted owls, and to identify likely factors that influence these patterns of abundance. I described absolute abundance using two scales of habitat classification, one that corresponded to a macro scale (i.e., habitat type), which embodied small mammal populations within discernable units of space defined by combinations of pertinent resources, and another corresponding to a micro scale (i.e., independent regressors), which was comprised of specific habitat attributes likely to be selected for use by individuals across populations. Abundance was also described according to two temporal scales, annually among six consecutive summers and seasonally within a single year.

The findings provide a quantitative picture of these species' distributions and abundance within the common habitats available to Mexican spotted owls in the Sacramento Mountains. The results also identify prominent factors that influence abundance of five murid rodents.

In general, regressors identified as having the most likely effects on biomass varied according to each species. Only the number of mature females in summer populations (MATFEM) proved to be a consistently strong influence (recall Table 2.23). This parameter was positively associated with summer biomass of all five species. However, magnitude of its influence varied slightly among species.

Aside from the number of mature females in a population, other top ranked regressor variables indicated that a differing array of biotic and abiotic factors influenced summer abundance of these five murid species. For example, deer mouse abundance was positively influenced by production of grasses and/or forbs, and by cold temperatures during late fall and winter periods. In contrast, brush mouse abundance was positively influenced by density of oaks (shrub-sized and trees) and negatively influenced by rock

cover. Mexican vole abundance was positively influenced by grass and/or forb production, and concurrent densities of long-tailed voles. Abundance of long-tailed voles was positively associated with density of Mexican voles, production of forbs and grasses, and negatively associated with amount of shrubs. Temperatures during fall and winter also appeared to influence abundance of long-tailed voles. Finally, abundance of Mexican woodrats seemed to be influenced by amount of rock cover, large logs, and shrubs.

Species-specific Evaluations

General distributions and macrohabitat associations of these five species did not deviate radically from other studies conducted in western montane systems (see species-specific reviews by Durrant 1952, Findley et al. 1975, Hoffmeister 1986, Fitzgerald et al. 1994). However, the demonstrated trends in abundance offer new information for some species and additional insights on factors influencing population dynamics for others. Pertinent findings and comparison with previous accounts are discussed below, according to species. The number of reproductively active females in summer populations with its common influence on abundance of all species, warrants special attention. This relationship will be discussed after the other factors that vary by species.

Deer mouse. This species was found commonly in all sampled habitats. Its nearly ubiquitous distribution supports previous claims that deer mice are habitat generalists, particularly when other species of *Peromyscus* are absent (Baker 1968). Findley et al. (1975) state that in central and southern New Mexico, deer mice are most abundant in montane conifer forests including pine types but rarely encountered in woodlands or upon rocky hillsides. I did find that deer mice were most abundant in

montane coniferous forests of the Sacramento Mountains but their abundance was also influenced by seral stage. Deer mice were usually more abundant in the mid-seral stage (60–100 yrs in age) of mixed-conifer forests. I also found deer mice regularly in xeric forests which included pinyon-juniper-oak woodlands and rocky hillsides, and in sympatry with brush mice. Although deer mice were not rare in the xeric forest they were fewer in abundance compared to habitats occurring at higher elevations. The distributional pattern of deer mice within the xeric forest was more in agreement with patterns described by Holbrook (1978) for sites in northern New Mexico.

Deer mouse abundance in the Sacramento Mountains was moderately high compared to other studies. Spring densities were generally higher than those summarized by Baker (1968), whereas fall densities were comparable. Summer densities ($\hat{D}$ ranged 0.2–60.9) exceeded the median of a broad range reported for other coniferous forest biomes. Gashwiler (1979) reported densities of 4.3–6.8 deer mice/ha from western Oregon, Goodwin and Hungerford (1979) reported approximately 1–20 deer mice/ha in northern Arizona, Merritt and Merritt (1980) reported densities of 2.5–26.7 deer mice/ha from the Front Range of Colorado, and Van Horne (1981) reported a range of 12.3–88.9 deer mice/ha for Prince of Wales Island, Alaska. Peak density (60.9 deer mice/ha) during the irruption within the mesic forest (summer of 1991) was well below the maximum density (462 deer mice/ha) reported for this species (e.g., in shrub habitats on Santa Barbara Island, California; Drost and Fellers 1991).

Seasonal and annual trends were similar to previous studies. Whether irruptions of the type observed in 1991 also occur in other regions was difficult to determine because most studies were of short duration (i.e., 2–4 years). However, Sullivan and

Krebs (1981) reported an eight-fold increase in clear-cuts following logging of coniferous forest in British Columbia, Canada. Also, approximate three to four-fold increases were observed in three seral stages of conifer forest of Southeast Alaska by Van Horne (1981). The latter increases resulted from high juvenile recruitment including immigration from a fourth seral stage of higher quality. The magnitude of the 1991 irruption in the Sacramento Mountains was nearly five-fold greater than average abundance in mesic forests during subsequent increases in 1994, and four-fold over the increase in 1996.

Causes of the irruption are unclear. It was not triggered by recent timber harvest. No harvest occurred in or near the mesic-forest sites immediately preceding or during the study. Nor did the irruption appear to be the consequence of recent immigration. On multiple occasions three or four juveniles or young subadults were captured together in one trap. Hence, it seems more reasonable to believe that high reproduction occurred in the sampled habitat, as opposed to mass immigration from another habitat.

Possible explanations for the irruption include an ample crop of conifer seed during fall of 1990 and/or less predation during breeding season of 1990. For example, rainfall during spring and summers of 1990 and 1991 exceed by 26% rainfall during the same period of other years, with the greatest amounts occurring in March and June of 1991. This may have stimulated early release of Douglas-fir seed, a common food of deer mice, during summer of 1991. In addition, no reproduction was observed for 39 pairs of Mexican spotted owls surveyed in 1990 (Lincoln National Forest, *unpublished data*), indicating that fewer numbers of prey would have been required or available to satisfy energetic needs of this predator during the 1990 breeding season. If spotted owls switched to other food sources, then more deer mice may have survived during the fall

1990-winter 1991 period. Thus, an abundant release of seed subsequent to a period of reduced predation and improved survival may have triggered additional litters by adult females or early reproduction in subadult females that lead to the irruption of 1991 in the mesic forest.

During 1992–1995, annual abundance of deer mice in different habitats fluctuated significantly and generally in synchrony. Statistically, there were no differences in abundance of this species among habitats but there were through time, suggesting that a common factor like weather may have influenced their population dynamics. Regression models showed that summer abundance of deer mice was positively correlated with rainfall from two previous growing seasons and negatively correlated with temperatures during preceding fall and winter periods. Thus, during at least three years of study (1992–1994) deer mouse populations increased in accordance with higher rainfall during two previous growing seasons and colder fall-winter periods.

Positive effects of rainfall on deer mice have been reported previously for studies conducted in more arid environments. The effect is often reported as indirect and manifested by the influence of rain on primary production. For example, Drost and Fellers (1991) found that deer mice decreased in abundance following winters of low rainfall when protective cover provided by plant growth diminished and subsequent predation by barn owls increased. Water stress played a minor role in population decrease because succulent cactus were used by deer mice during drought periods (Drost and Fellers 1991). Beatley (1969) found that spring reproduction and summer rodent densities in a Mojave desert community were positively correlated with previous fall rains that permitted adequate germination of annual plants through that same fall and

subsequent winter. In shrub and grassland communities of southern New Mexico, Ernest et al. (2000) found positive correlations between plant growth and precipitation during the same growing season. They also documented positive correlations between precipitation in a previous season or past two seasons (~1-yr lag) and density of all rodents (including deer mice), and between rodent density and plant cover during previous seasons. When examined, significant correlations have not been found between deer mouse density or reproduction and precipitation in more mesic coniferous forests of western coastal regions (Sadlier 1974, Van Horne 1981). In the present study, a positive correlation between summer biomass of deer mice and precipitation during two previous growing seasons corresponds with requirements for production of seed by several conifer species and represents a protracted time-lag (~2-yrs) compared to that found in more xeric environments. Thus, the less-immediate response by deer mice to previous rainfall in the Sacramento Mountains seems intermediate compared to more rapid responses seen in arid environments and undetectable responses seen in more mesic environments.

Positive increase by deer mice to colder fall-winter temperatures is counter to that predicted according to potential energetic demand. The observed relationship would seem reasonable if colder temperatures corresponded with increased snowfall that in turn provided thermal insulation and protection from avian predation (Spencer 1984, Hannson and Henttenon 1985). However, snowfall was sporadic during these periods and information on trends in snow depth was too limited to evaluate the relationship further. Another possibility is that the association reflects some other effect related to elevation, which was used to predict fall-winter temperature values. For example, the pattern could reflect the distribution of brush mice. Summer abundance of the latter species was

inversely related to elevation. It might also correspond to mesic vegetative conditions or distribution of Douglas-fir. Availability of Douglas-fir seeds has been linked to deer mouse abundance (Gashwiler 1979). However, evidence of direct correlation between summer abundance of deer mice and elevation was weak ($r = 0.35$; $P = 0.122$). A more plausible explanation is that colder temperatures during fall caused breeding to cease early, reducing competition for food or den sites, which in turn, allowed subadults to overwinter and emerge as adults in better condition the following spring (Van Horne 1982, Millar 1984, Millar and Teferi 1993).

Abundance of deer mice did not covary with many microhabitat attributes. This finding concurs with behavior anticipated for a generalist and the observed lack of difference in abundance among macrohabitat types, which do vary according to microhabitat components. Regression model results suggested that summer abundance of deer mice was positively influenced by production of grasses or forbs and possibly abundance of mature conifers. Both were predicted to be important sources of food for this mouse. An *ad hoc* correlation indicated that volume of slightly decomposed, large logs might also influence abundance of deer mice. This variable is supposedly related to cover and substrate for foods like arthropods or fungi. In comparing numbers of individuals captured at trapping stations, among four different seral stages of conifer forest, Van Horne (1981) found negative correlations between herbaceous cover and abundance of juvenile deer mice and nonsignificant correlations with abundance of adults. She also found a significant positive relationship with tree canopy closure (160 cm above the ground) and density of adult deer mice but a weak negative relationship with juvenile abundance. Relationships with log cover were non-significant. In pine

forests of northern Arizona, Goodwin and Hungerford (1979) did not find significant relationships between herbaceous cover or tree density and abundance of deer mice, but did report a nearly perfect correlation ($r = 0.99$) with log volume. These discrepancies could represent different methodologies used to sample microhabitat features or estimate rodent abundance, real geographic or community variation, density-dependent shifts in habitat use, or spurious associations.

A multitude of multivariate analyses on microhabitat selection by deer mice have been conducted (e.g., see review by Kaufman and Kaufman 1989). However, I do not reference these findings here because it is difficult to interpret the influence of singular components on abundance from these types of analysis and because scales of the response variable differed from the present study (occurrence versus abundance). Implications of the associations between abundance of deer mice and particular microhabitat components are discussed collectively with results from other rodent species, below.

Brush mice. This species of mouse was found predominately in the xeric forest and only rarely in the mesic forest. When brush mice did occur in the latter habitat, they were found in small pockets of low-growing oaks near rock outcrops or ridge tops. Brush mice were not encountered in meadows. This distribution matches that given by Findley et al. (1975) for New Mexico and that given for brush mice occurring in multiple regions of its range (Jameson 1951, Brown 1964a, Armstrong 1979, Holbrook 1979a, Svoboda et al. 1988, Sureda and Morrison 1998).

Brush mouse abundance in the Sacramento Mountains was similar to reports for other populations. Spring (1.9; 4.4 mice/ha), winter (2.4; 7.4 mice/ha), and fall (2.1; 3.4 mice/ha) densities for two populations during one year in the xeric forest were within the

range of estimates from two other studies. Brown (1964b) reported spring (2.0 mice/ha), winter (1.1; 5.2 mice/ha), and fall (0.7; 2.1 mice/ha) densities during two years for one population occurring in juniper glades interspersed with rocky outcrops in Missouri. Ellison and Van Riper (1998) reported spring (7.6; 8.0 mice/ha) and winter (7.6 mice/ha) densities for a population occupying a desert-riparian terrace in central Arizona. Similar to the population studied by Brown (1964b), I found that brush mice may sometimes be more numerous during winter periods than preceding fall or subsequent spring periods. Summer densities ($\hat{D}$ ranged 0.16–23.19 mice/ha) from the present study also fell within the range reported by others. Ellison and Van Riper (1998) reported summer densities of 0.9–6.2 mice/ha, Holbrook (1979b) reported summer densities of 12.7–31.3 mice/ha for several grids in a habitat similar to xeric forest of the present study, and Goodwin and Hungerford (1979) found 1.2–48.9 mice/ha occupying woodlands and forest of northern Arizona usually dominated by ponderosa pine. Estimates from the latter study are ecological densities (number per area of occupied habitat) which overestimate crude densities like those given for other studies. These comparisons of brush mouse abundance show higher peak densities occurring in montane woodlands.

No irruptions or excessive peaks in brush mouse abundance were detected during this study. Other long term (>3 yrs) studies reporting trends in brush mouse abundance were not found. During 1992–1995, interaction between temporal and habitat-related factors influenced variation in summer abundance. This interaction was significant because abundance of brush mice in the xeric forest was always greater than in other habitats and fluctuated annually while abundance in other habitats did not change.

Results from linear models indicated that none of the selected weather variables

was a strong predictor of summer abundance of brush mice. This differs from Goodwin and Hungerford (1979) who implicated harsh winters as a force of decline in brush mouse populations. Winter conditions during 1992–1994 in the Sacramento Mountains may not have approached the same "harshness" experienced by brush mice in the former study. However, *a posteriori* examination of data from all years and sites showed maximum summer abundance when minimum temperatures during late fall-winter periods approached moderate levels (−5 °C to −6 °C). Hence, the lack of prediction strength with winter condition could be due to a non-linear relationship, which was not incorporated into the model. Rainfall during two previous growing seasons also showed a non-linear relationship with summer abundance of brush mouse. Although the correlation signified a negative relationship, closer inspection of the bivariate plot (recall Fig. 2.15) reveals a bimodal and positive relationship, which is dependent upon year. During some years the increase with previous rainfall is greater. One possible explanation is brush mouse response to mast production, which is a function not only of previous rainfall but also time since last seeding (Sork et al. 1993). It could also reflect response to different food sources that vary in different ways with precipitation or the influence of food availability and temperature on reproduction (e.g., see Bronson and Pryor 1983).

Two microhabitat regressors, percentage of rock cover and density of oaks, provided moderately strong predictions of brush mouse abundance. The relationship was predicated on variation among sites, rather than temporal changes in rock cover and oak density. Sites with greater rock cover likely offered greater protection from predators and more dens. Many of the xeric forest sites included ribbons of limestone interspersed

among junipers, pinyons, other pines, and shrub-like oaks. Limestone extrusions often formed horizontal overhangs close to the ground and were incised with vertical crevices. Released brush mice frequently returned to these types of shelters. Brown (1964b) and Goodwin and Hungerford (1979) found similar use of rock outcrops or piles and suggested that these structures help explain variation in distribution and abundance of brush mice.

Oaks likely provided food and foraging cover. Temporal trend in mast production was not quantified during this study. However, I noted that grey oaks produced acorns at most of the xeric trapping sites during 1991 and 1996 but not during other years. Peak abundance of brush mice found in this study occurred in the summer of 1992 (recall Fig. 2.10), and may have been a response to mast production. Wolff (1996) was able to predict summer abundance of white-footed mice (*P. leucopus*) and deer mice from acorn crops during a previous fall. In his study, mice bred all winter following good acorn crops, which lead to increased numbers of mice in the subsequent summer. Unfortunately, abundance of brush mice during summer of 1997 was not sampled in the Sacramento Mountains and therefore it is unknown if the prediction was supported further.

Mexican voles. Little has been documented about the population ecology of this species. Hence, findings regarding spatial variation in population abundance and multiannual trends are novel for the species. An envirogram depicting factors that influence Mexican vole abundance was modeled in large part on ecology of meadow voles. It therefore seems appropriate to compare the two vole species.

Mexican voles occurred primarily in montane meadows of the Sacramento

Mountains. The species was also found in mesic and xeric forests but occurrence and abundance in this habitat corresponded with high abundance in montane meadows and was probably a consequence of immigration (Wilhelm 1979). When biomass in montane meadows dropped below 1 kg/ha, no Mexican voles were found in the two forested habitats (recall Fig. 2.10). Mexican voles were found in association with long-tailed voles which occupied the same meadows and mesic forest habitat. This description of Mexican vole distribution fits precisely that given by Findley et al. (1975). Conley (1976) found Mexican voles in a montane meadow of the Sacramento Mountains, but did not find them in adjacent mixed-conifer forest. Summer abundance during his study would have been ≤840 g/ha assuming mean mass of 28 g/individual. Mexican voles have also been collected from lower elevations than at locations in the present study (i.e., <2100 m) and in more xeric conditions (Frey and LaRue 1993, Kime et al. 1995).

Estimates of absolute abundance of Mexican voles exist only from one other published study (Conley 1976). In a meadow at Potato Canyon, Sacramento Mountains, Conely (1976) found that abundance peaked in October 1969 (44 voles/ha) following gradual increase during summer. A rapid decline ensued in November 1969. Then, following gradual increase during spring and early summer, Mexican vole abundance peaked again in mid-July 1970 at 38 voles/ha. Estimates from the present study showed similar seasonal trends during fall of 1993 through summer 1994. However, summer abundance of Mexican voles in 1994 was lowest of five summers examined, and hence, the seasonal trends likely represented fluctuations occurring during a period of low abundance or a decline phase like that observed by Conley (1976). Abundance of Mexican voles in meadows during other summers were usually greater ($\bar{D}$ = 90.2

voles/ha). Peak abundance of Mexican voles for each of five sites throughout the study period ranged (94.2–183.4 voles/ha; $\hat{D}$). These values fall within bounds for densities of cyclic and non-cyclic populations of meadow voles in various habitats (Taitt and Krebs 1985, Getz et al. 2001). At a sixth site, sampled during three summers (1992–1994), Mexican vole abundance ($\hat{D}$) ranged 0–8.7 voles/ha. This site was heavily grazed by ungulates and height of herbaceous plants was consistently low.

Conley (1976) assumed that his study population of Mexican voles cycled. In their review of vole population dynamics, Taitt and Krebs (1985) explained that vole populations may undergo both multiannual (cyclic) fluctuations and/or annual fluctuations. The former are defined by a low-peak-decline sequence occurring over at least two years and peak phases are preceded by slight spring declines only in the number of males in the population. Frequency of cyclic peaks is commonly 3–4 yrs in populations of North American voles that do cycle. Annual fluctuations simply show seasonal increases each year with peaks preceded by spring declines of both sexes. Numerical change is usually >10-fold during a complete phase of a multiannual cycle and <five-fold during an annual fluctuation. Also, variation in peak densities among years are >three-fold for populations experiencing multiannual cycles. Using these criteria, Taitt and Krebs (1985) classified the fluctuations reported by Conley (1976) as annual fluctuations.

Population trends from the present study indicate, however, that some Mexican vole populations in the Sacramento Mountains may exhibit multiannual fluctuations. Cyclicity indexes (standard deviation of mean [$\log_{10}$ of density]) measure the amplitude of fluctuation and are sometimes useful in distinguishing cyclic from non-cyclic

populations (Hannson and Henttonen 1998, but see Getz et al. 2001). Two meadow populations of Mexican voles scored 0.46 and 0.52 over three years of measurement. Summer density at these two sites ranged 14.0–94.2 voles/ha and 18.9–183.4 voles/ha, respectively. The index scores are similar to those for cyclic populations of red-backed voles (*Clethrionomys glareolus*) and field voles (*Microtus agrestis*) occurring in northern regions of Scandinavia (Hannson and Henttonen 1998). Differences between the summer population peaks are 6.7- and 9.7-fold, respectively. However, population condition during spring of the increase phase was unknown. Three other populations of Mexican voles scored 0.31, 0.28, and 0.16 over 3, 5, and 4 yrs respectively. Fluctuations of all populations were in synchrony. Variation in amplitude reflects variation in amount of herbaceous cover among meadows (see below). Investigation of these populations at more frequent and longer time periods will certainly be required to verify whether Mexican vole populations cycle in the Sacramento Mountains (Getz et al. 2001).

The significant interaction between temporal and spatial effects on summer abundance of Mexican voles was similar to that found for the brush mouse. That is, abundance in the primary habitat, in this case meadows, fluctuated significantly through time while populations in other habitats changed only slightly. The pattern seems consistent with the idea that montane meadows comprise the primary habitat of Mexican voles in the Sacramento Mountains and that other habitats may be dispersal sinks. Similar patterns have been observed for meadow voles that disperse into adjacent woodlands in relation to abundance in preferred grassland habitat (Grant 1971, Tamarin et al. 1984, Adler and Wilson 1989).

High weighting of the global regression model for predicting abundance of

Mexican voles indicates that several factors may influence change in this species' abundance. One of three top ranked regressors was abundance of a common competitor, the long-tailed vole. Abundance of long-tailed voles corresponded to higher abundance in Mexican vole populations. These two species compete for space and long-tailed voles are usually dominant over Mexican voles (Conley 1976). As abundance of long-tailed voles increased, dispersal of Mexican voles may have been limited, effectively concentrating the latter and increasing its density. Thus, abundant long-tailed vole populations may have stimulated a fence effect (Lidicker 1985). In this case, the fence would be a behavioral barrier like that stimulated by social classes (Hestbeck 1982) rather than a physical barrier. The effect does not increase actual numbers of Mexican voles. Rather, the presence of long-tailed voles probably restricts access of space by emigrating Mexican voles through occupancy of the area and aggressive behavior (Conley 1976). Avoidance behavior by Mexican voles may also contribute to the effect. The consequence is that Mexican vole populations that are increasing by independent means become concentrated. Disruption of dispersal and the resulting influence on increasing populations is well known for several vole species studied in enclosures (Lidicker 1985). Effects of interference competition among sympatric vole species has also been offered as a mechanism explaining habitat use and distribution (Findley 1954, Grant 1969, Randall 1978, Randall and Johnson 1979, Madison 1985). However, the extent that interaction between dispersal and interference competition can regulate or otherwise influence population process of sympatric vole species is not well known and deserves additional study. An alternative explanation is that environmental conditions caused independent but synchronous trends in populations of both vole species. However, populations of

these two vole species were not in synchrony during the last two years of study.

Abundance of long-tailed voles did not appear great enough to trigger suppression of Mexican vole reproduction, as proposed by Conley (1976) for situations when both populations reach peak abundance during an increase phase. Variation in the bivariate plot of abundance of both species (recall Figure 2.16) did not show a slower rate of change in Mexican vole abundance at peak abundances of long-tailed voles during summer periods. However, this simple relationship might not account for delayed effects realized in subsequent seasons.

Production of grasses and forbs had a strong positive association with summer abundance of Mexican voles. Explanation for the relationship is one of the most basic in ecology—voles require herbaceous vegetation for food and cover (Birney et al. 1976, Rose and Birney 1985). In the present study, 6.6 cm of mean maximum height of summer grasses or forbs was a threshold, above which Mexican vole abundance increased with increasing height of herbaceous vegetation during summer months (recall Fig. 2.16). It is unknown if the increase is related to increase in certain food plants, protective cover, or both. Experimental work has shown that supplemental cover can elicit greater responses in meadow vole abundance than addition of quality food (Peles and Barrett 1996). Whatever the underlying reason, the relationship is predominant among other factors. Approximately 83% of the variation is explained by a simple linear regression of Mexican vole biomass on mean maximum grass-forb height during the summer period compared to 96% for the highly weighted global model (with seven ecological regressors) for this species. Thus, variation in amount of herbaceous vegetation among sites probably contributed greatly to the variable amplitudes observed in population

fluctuations of this species, as has been shown for meadow vole populations in Illinois (Getz et al. 2001).

Several other microhabitat descriptors were found to be associated with summer abundance of Mexican voles (recall Fig. 2.17). However, all of these can be explained by ancillary relationships with herbaceous vegetation. For example, negative relationships between Mexican vole abundance and shrub and tree cover reflect the absence of dense herbaceous cover.

Long-tailed voles. Distribution of this vole was bimodal, occurring commonly in meadow and mesic forest habitats. Only one individual was observed in a xeric forest throughout the study period. Findley et al. (1975) describe the vole as a montane forest species dwelling in meadows, forest edges, and sometimes forest interior. This description applies well to long-tailed voles in the Sacramento Mountains. On average, abundance was greater in meadows (recall Table 2.8) than in either mid-seral or late-seral mesic forest. Grids were placed within meadows or forest types rather than spanning ecotones. Nonetheless, spatial distribution of captures within grids showed long-tailed voles distributed toward meadow edges, rather than within meadow interiors. A similar pattern was observed in some forest grids; long-tailed voles were concentrated away from upland slopes and on portions of the grid nearer to forest-meadow boundaries. These patterns suggest that long-tailed voles in the Sacramento Mountains may also occupy forest-meadow ecotones.

In contrast to my findings, Conely (1976) did not find long-tailed voles of the Sacramento Mountains in mixed-conifer forests adjacent to the meadow he sampled during 1969 and 1970. In his study of one meadow, long-tailed voles attained a peak

density of 118 voles/ha. Also in contrast to my study, other authors found that long-tailed voles avoided or existed in low abundance within late-seral stages of conifer forest (Halvorson 1982, Van Horne 1982b). Although I recorded low abundance of long-tailed voles occupying two late-seral forest sites during two of three summers (1994 and 1995), I also found moderate numbers of this vole ($\hat{D}$ = 12.4 voles/ha) at one late-seral forest site during summer of 1996 (the second site was not sampled in 1996). At this time, long-tailed voles were significantly more abundant than in other habitats ($\hat{D}$ = 6.9 and 1.1 voles/ha in mid-seral mesic forest and meadow, respectively). Thus, common distribution patterns for this species may vary over time. In such cases, short-term studies could lead to erroneous conclusions about habitat preference by this species. Cause for the shift in distribution is unknown, but greater abundance at this late-seral forest site followed a summer when abundance was low in all habitats (all $\hat{D}$ <2.6/ha; recall Fig. 2.10). The shift in distribution may also be attributed to interaction with Mexican vole populations, which generally exceeded abundance per unit area of long-tailed voles dwelling in meadows.

Seasonal estimates of abundance recorded for a low population phase were below values reported by previous studies. Fall estimates ($\hat{D}$) ranged from 0–1.7 voles/ha, winter estimates range 0–0.3 voles/ha, and spring estimates ranged from 0–0.5 voles/ha at two meadow sites and at two mid-seral mesic forest sites. Conley (1976) observed a declining population in November 1969 at 38 voles/ha and at 16 voles/ha in the following May. Van Horne (1982b) found fall densities of ~11–24 voles/ha and spring densities of ~3–14 voles/ha over two years in three young seral stages of conifer forest in Southeast Alaska. She also found fall densities of ~4 and 5 voles/ha, and spring densities of ~1 and

4 voles/ha in late seral forest. These populations appeared to undergo noncyclic, annual fluctuations. Cranford (1984) reported densities ranging 3.6–12.6 voles/ha during March–June and 0.4–7.1 voles/ha during November–February occurring over three years in subalpine meadows of Utah.

Most of the summer estimates of abundance from the present study spanned those reported by others but peak densities were usually greater. In my study, summer densities ($\hat{D}$) of populations in meadows ranged 1.1–54.0 voles/ha whereas summer densities of populations in mid-seral mesic forest ranged 0.3–33.8 voles/ha. Van Horne (1982b) reported summer densities of ~2–18 voles/ha in early seral stages of conifer forest and 0 and ~4 voles/ha in late seral forest. Cranford (1984) reported densities during July–October of 5.0–28.5 voles/ha. Thus, only Conley (1976) has observed greater summer densities of long-tailed voles and these also occurred in a meadow of the Sacramento Mountains.

Conely (1976) considered his study population of long-tailed voles to be cyclic. Taitt and Krebs (1985) listed Conley's classification as questionable given lack of information on spring densities. Their review of other studies suggested that long-tailed voles did not undergo multiannual cycles. Fluctuations reported for long-tailed voles by Van Horne (1982b) appear to be non-cyclic. Numerical trends of long-tailed voles dwelling in shrub dominated habitats of eastern Washington (Randal and Johnson 1979) resemble the frequency but not the amplitude of a cyclic population. My findings indicate some populations of long-tailed voles may cycle, as originally suggested by Conley (1976). For example, cyclicity scores were 0.66 and 0.80 for two populations occupying mid-seral mesic forest 0.32, 0.37, 0.55, 0.56, and 0.76 for populations occupying

meadows, and 0.54 for one population occupying late-seral mesic forest. Peak summer densities of populations within each habitat type (5.4–54.0 voles/ha in meadows; 0.3–33.8 voles/ha) were lower than those reported for Mexican vole populations in the same mountain range and did not approach those typically associated with cyclic populations (Taitt and Krebs 1985). However, because long-tailed voles typically attain maximum abundance in September or October (Johnson and Randall 1979, Cranford 1984), I may have underestimated the full magnitude of their increase. Clearly, longer term, more frequent observations are needed to characterize population trends of long-tailed voles (Getz et al. 2001).

A significant interaction among temporal and habitat-related effects on long-tailed vole abundance (summers 1992–1995) was reported here. The interaction occurred between stable trends of no occupancy in xeric forests while slightly different sized populations in meadows and mid-seral mesic forest declined in synchrony from 1992 to 1994, and then remained low in all habitats during summer of 1995.

Several ecological factors appeared to influence abundance of long-tailed voles. One of five heavily ranked factors was minimum temperatures during late fall through winter. An optimum of summer abundance appeared between −6 and −7 °C. It is unknown if this reflects an optimal energetic range during over winter periods, but it is unlikely. Beck and Anthony (1971) found that long-tailed voles acclimated to natural winter temperatures of 11 °C required energy expenditure to maintain homeothermy when in a nest and temperature fell below 20 °C. An alternative explanation is that the relationship reflects periods when snow cover was present. Snow cover provides protection from predators and insulation (Spencer 1984, Hannson and Henttenon 1985).

Cranford (1984) reported that delayed snowfall resulted in colder ground temperatures (−20 °C to −10 °C), which increases overwinter mortality and eventually low abundance in subsequent spring or summer. However, snowfall was sporadic during the study period and information on trends in snow depth was too limited to evaluate the relationship further.

Two microhabitat components ranked high in predicting long-tailed vole abundance; shrub density and grass-forb height. However, abundance of shrubs had a negative influence on long-tailed vole density, which was counter to what Van Horne (1982b) observed for populations inhabiting young seral stages of conifer forest in Alaska. In the Sacramento Mountains, forbs may be a more common food source than shrub fruits or mast. The relationship between long-tailed vole abundance and grass-forb height in the present study was positive but much more variable than that with Mexican vole abundance. A simple linear relationship with grass-forb height in this case would only explain 26% of the variation in summer abundance of long-tailed voles compared to 83% in abundance of Mexican voles. The difference may reflect a greater attraction to forbs for food and cover rather than grasses. Forbs can be found under forest canopy proximal to meadow-forest ecotones in addition to meadow interiors. Herbaceous cover dominated by forbs was also found within canopy gaps of the late seral forest where long-tailed vole abundance exceeded other habitats in summer of 1996. Halvorson (1982) found the greatest numbers of long-tailed voles in his study within a burned clear-cut with ample herbaceous cover.

Density of Mexican voles was also associated with long-tailed vole abundance. The relationship implies interference competition but may simply mirror the fence effect

reported for Mexican voles occurring in meadows. Long-tailed voles are capable of using meadow and portions of forested habitat, and hence their dispersal space may not be limited. However, if both habitats were saturated with long-tailed voles, and Mexican vole abundance in meadows was concurrently great, the fence could become mutual. For the effect to be mutual, long-tailed voles would have to avoid Mexican voles. Randall (1978) found that long-tailed voles preferred grassy habitats but used shrub-dominated habitats when montane voles were present. It is uncertain which habitat (mesic forest versus meadow) is preferred by long-tailed voles in the Sacramento Mountains. However, greater abundance was most often observed in meadows. Although long-tailed voles are larger and behaviorally dominant over Mexican voles (Conley 1976), use of a forest habitat by long-tailed voles may be a form of avoidance behavior that saves energy.

Precipitation may also have influenced long-tailed vole abundance. Cumulative rainfall during a preceding spring, and cumulative rainfall during a previous summer through to a recent spring were positively correlated with this vole's abundance in summer. Long-tailed voles require mesic conditions and lush vegetation. Water deprivation over short periods can be fatal (Findley et al. 1975). The relationship with previous rainfall may express this vole's water requirements. Alternatively, it may reflect an indirect influence on production of the vole's food and cover.

Mexican woodrat. This woodrat occurred in all sampled habitats. However, individuals captured in meadow habitats usually were also captured in adjacent mesic forest or associated ecotones. The Mexican woodrat was slightly more abundant in xeric forest during most of the study (recall Fig. 2.10). This finding varies from Findley et al. (1975), who stated that Mexican woodrats reached greatest abundance in montane mixed

conifer forest.

Long-term (>3yrs) estimates of absolute abundance presented here appear to be novel for this species of woodrat. I found only one other study reporting absolute abundance for this species (Goodwin and Hungerford 1979). Thus, I also reference studies on other woodrats dwelling in western forest biomes for comparison. In general, seasonal estimates were similar to other species. Abundance ($\hat{D}$) of Mexican woodrats in forested habitats of this study ranged 0.3–2.2 woodrats/ha during one fall, 0–0.8 woodrats/ha during one winter, and 0–0.5 woodrats/ha during one spring. Carey et al. (1999) reported 0.2–4.2 dusky-footed woodrats/ha and 0.2–1.3 bushy-tailed woodrats during spring or fall in mixed-conifer forests of Oregon and Washington.

Estimates of summer abundance were also generally similar to those of other woodrats, except compared to those dwelling in oak woodlands or shrub dominated habitats. During the course of this study, summer density of Mexican woodrats ranged 0.3–3.1 woodrats/ha in mid-seral mesic forest, 0.5–1.9 woodrats/ha in late-seral mesic forest, and 0.3–3.3 woodrats/ha in xeric forest. Goodwin and Hungerford (1979) reported summer (ecological) densities of Mexican woodrats of 4.9–24.7/ha in rocky canyons of ponderosa pine forest, northern Arizona, and 4.9–27.2/ha in manipulated forest treatments with slash piles. Sakai and Noon (1993) and Ward et al. (1998) reported mean summer densities of 0.41 and 0.90 dusky footed woodrats/ha, respectively, in late-seral mixed-evergreen forest of northwestern California. Sakai and Noon (1993) also reported extreme summer densities of 81.1 dusky footed woodrats/ha in sapling/brush dominated seral stages. Linsdale and Tevis (1951) reported 8.2 and 11.2 dusky footed woodrats for two summers in habitat comprised of oak woodland and chaparral.

Variation in summer abundance of Mexican woodrats was due primarily to differences among habitat types. Significant differences were mainly between forest habitats and meadows. Annual variation was nearly significant. There was no interaction effect on Mexican woodrat abundance. Linsdale and Tevis (1951) reported only slight variation among estimates of dusky footed woodrat abundance in April over four consecutive years (6.9, 5.7, 5.6, and 6.8 woodrats/ha). The limited information suggests that woodrats are not prone to wide changes in abundance characteristic of smaller rodents.

Three microhabitat features were ranked as relatively likely influences on summer abundance of Mexican woodrats. These included amount of rock cover, density of large logs, and density of shrubs. However, these relationships were not exceptionally dominant (recall Fig.2.20). Boulder piles and canyon walls with crevices are important features that provide dens for Mexican woodrats (Finley 1958). However, the weak relationship may be in the way rock cover was indexed. Percentage of rock cover did not distinguish bare rocky surface from boulders. Large logs are also important sources of cover for woodrats, during movement and for dens. Shrubs are a common food source (Finley 1958). However, relationships with these two variables appeared slightly negative. Extreme shrub densities were recorded for sites with an abundance of low growing oaks. Foliage of oaks can contain high levels of secondary compounds like tannins and no palatable fiber. In some situations, ingestion of tannins may be fatal (Voltura and Wunder 1994). Thus, low woodrat abundance in areas of very dense oaks may represent an aversion to sites with low quality food.

No weather variables were ranked as important influences. However, three of the

a posteriori relationships implicated additional microhabitat effects that are worthy of mention. Percent tree cover and density of snags from deciduous trees showed a quadratic relationship with average biomass of Mexican woodrats (recall Fig. 2.21). Moderate amounts of tree cover and moderate amounts of snags corresponded to higher woodrat abundance. Both sets of relationships may be indicative of use of alternative den sites in absence of rocky shelters. The relationships may also optimal combinations of food supply (i.e., conifer needles, shrubs, and forbs). Mexican woodrat abundance also increased asymptotically with volume of large, undecomposed logs, and as a quadratic function with volume of large highly decomposed logs. These two relationships may also reflect a benefit from moderate amounts of logs for use as cover and for dens in absence of rock shelters. Sites with greater densities of logs and low numbers of Mexican woodrats may reflect areas lacking desirable amounts of tree cover (e.g., large open gaps), shrubs, or forbs. The nonlinear relationships between abundance of logs and snags with Mexican woodrat abundance suggest that lack of den sites alone is probably not limiting this woodrat's abundance. Rather, lack of den sites within close proximity to suitable food sources may be a limiting factor.

Procedural and Alternative Effects

Enumeration errors for population size (and hence for density) may not have been estimated accurately. Simulations have shown that the model-selection procedure performs poorly when the number of marked individuals is <100 and capture probabilities are <0.30. Incorrect model selection can produce bias in either direction (White et al. 1982, Menkens and Anderson 1988). For enumeration errors of population sizes <100 individuals to be unbiased and minimal, p should approach 0.50 (White et al. 1982).

Although <8% of the data sets met the conditions necessary for estimating confidence limits of population size without bias (Fig. 2.8b), the CAPTURE-based estimates of population size were still considered more reliable for estimating density than the minimum number alive (a known underestimate of population size without any means for assessing enumeration error).

The assumption that maximum distance moved reflected home-range size was probably met for some species when population numbers were high and movements were restricted. However, when numbers were low and not confined by conspecific individuals, or when agonistic behavior in abundant populations caused greater movements, the maximum distance moved may have been underestimated, and hence, densities overestimated.

Tests for difference in species abundance among habitats or summers likely suffered low power in detecting all but large differences. Sample sizes for these tests were limited to three replicates of biomass per habitat and summer. However, the purpose of the tests was to gauge relative magnitude of influence by spatial versus temporal factors on each rodent's abundance. The key conclusion from this analysis was that the magnitude of spatial and temporal variation in abundance was not similar among the five rodent species, rather than inferring that space or time did not affect a species abundance. Thus, Type II error was of little concern in this analysis.

Finding strong regressors does not prove causation. The modeled relationships presented here are correlative. However, great care was taken to analyze factors that have *a priori* ecological justification. Envirograms were found to be useful in guiding model structure. Nonetheless, failure to include a variable in a final model set does not refute its

potential effect. The model procedure is based on the principle of parsimony. Thus, exclusion simply means that the information provided by the excluded effect was not necessary for producing an efficient description of the modeled relationship. Here efficiency means striking a balance between precision (high consistency) and accuracy (representing theoretical truth).

Some credible effects may have been underrated or not detected. This can happen when an inappropriate scale is used to model an effect. For example, abundance of alternative prey from each sampling site during a previous summer was considered an indirect measure of predator release. However, this regressor was never ranked as a strong effect. It could be that abundance of all prey available to all predators using the sampled site was needed to detect fully the release from predation. Also, time-intervals imposed by sampling may have been inappropriate for detecting some effects. For example, delayed density-dependence is often found to influence rodent demographics. With the exception of one species (Mexican vole) this effect was not strong enough to be rated important. Two explanations can be offered. First, the time-lag applied in all models was one year in duration and may have been too long to show an effect. Kesner and Linzey (1997) found that variation in density of white-footed mice was best described by seasonal (1-mo) time lags. Other studies however have reported one-yr lags in effects of density on rodent demographics (Fryxell et al. 1998, Lima et al. 1999). Second, density-dependent effects may only occur at high population levels. Data input into models spanned 1992–1994 and only in 1992 did abundance for two species (Mexican vole and long-tailed vole) indicate excess. Interestingly, delayed density dependence was indicated as an effect in populations of Mexican voles, the species which attained greatest

abundance.

Finally, effects inferred from the models presented here may not apply to different time periods that result in different ecological conditions. For example, findings regarding factors that influence deer mouse abundance apply to a period of low abundance (summers of 1992 and 1993) followed by a moderate increase (summer 1994). In contrast, asynchrony among habitats appears when data from 1991 and 1996 are considered, indicating that either the suspected influences of precipitation may not always apply to deer mice in all of the studied habitats or that the effects of other temporally related factors (e.g., predation, competition) may vary significantly among habitats in some years. Shifts in habitat-abundance relationships of some rodents have been documented following drought or excessive precipitation and corresponding extreme changes in rodent density (Van Horne et al. 1997, Gonzalez et al. 2000). Although effects reported here are based on models that incorporate both temporal and spatial variation in ecological condition, results based on great changes in abundance during the sampling period, like those for the two vole species, are probably the most reliable.

Evaluation of Common Effects

One factor appeared to exert a common influence on abundance of these five rodent species. The number of sexually mature females in the summer population was positively associated with summer abundance (biomass) of each species. Scores of relative importance for this regressor attained a maximum possible value of 1 in all but one set of models (recall Table 2.23). In addition, coefficient estimates averaged across model sets were exceptionally precise (CV<24%). Such a consistent result begs

consideration as an analytical artifact.

The strong relationship may stem from autocorrelation. For example, MATFEM (a regressor variable) was measured as the number of pregnant or lactating females in each population and was a subset of the total number of marked individuals used to estimate density. In turn, biomass (the dependent variable) was estimated from density. However, the effect also has a well known and obvious biological basis. Increase in population size is predicated on reproduction or immigration (Hoffmann 1958). Sexually mature females are not only the basic vessel of reproduction but often a stimulus for male immigration (Boonstra and Rodd 1983). A strong relationship between numbers of mature females and abundance should be expected among groups of animals like rodents that have life-history strategies favoring reproduction over longevity. Using the number of mature females from an earlier time period would offer a more appropriate measure that avoids the autocorrelation. However, abundance outside of summer could not be sampled every year. Although contribution by autocorrelation cannot be partitioned and evaluated relative to contribution by the real biological effect, I am content to consider the modeled effect as meaningful, particularly for discussing relevance of other identified factors.

Another important commonality among model results is identification of at least one microhabitat component as a predictor of rodent abundance. For three species, herbaceous cover was positively associated with their population abundance. For two other species, components describing rock cover and amount of shrubs were correlated. These relationships suggest two general assemblages of prey for the Mexican spotted owl. Three (deer mouse, Mexican vole, and long-tailed vole) predominate in higher elevations

or mesic locations and depend on production of herbaceous plants for food and/or cover. Two others (brush mouse and Mexican woodrat) predominate at drier, rockier locations that require a shrub or oak component for food. This perspective may be useful for identifying portions of a landscape and its potential for production of the owl's prey.

Implications

Estimates of biomass of these five rodent species over time and place describe the nature of food resources for Mexican spotted owls occupying the Sacramento Mountains. The population dynamics of these five species are mildly asynchronous through time, a condition that may be beneficial to spotted owls. Population dynamics of some of the species may also vary among macrohabitats. In general, the patterns portray a food base that fluctuates dynamically over short periods of time. The owl's response to these dynamics will be examined in Chapter 3.

The intended purpose of the modeling procedure was to identify key microhabitat features that might be targeted in future manipulations to sustain or increase abundance of desired small mammals. Identification of at least one microhabitat feature as a top-ranked regressor from models for each species generally supports the hypothesis that habitat manipulations may enhance the owl's common food resources. However, the ultimate evaluation must stem from experimental manipulation of the identified microhabitat features. Because parsimonious models included multiple factors, concurrent monitoring of these other key factors (e.g., number of mature females, weather) will be necessary for interpreting responses to microhabitat manipulations.

Species for which models demonstrated relatively stronger microhabitat effects

may offer the greatest chance for response to designed manipulations. For example, species affected primarily by weather or competition and weakly by microhabitat would not be expected to show strong responses to simple habitat manipulations. Given the strength of microhabitat regressors, overall model structure and ease of manipulating identified microhabitat features, I propose that ability to obtain responses through manipulations will be strongest for Mexican voles, followed by long-tailed voles, Mexican woodrats, deer mice, and weakest for brush mice.

Having identified relevant microhabitat components, particular disturbances or manipulations that may in turn influence abundances of these rodents can be identified. For example, given the model describing abundance of Mexican voles in Table 2.23, experimental manipulations that increase production of summer grasses and forbs (as measured by height) should produce an increase in vole biomass, when (1) numbers of mature females are also abundant and (2) long-tailed vole populations are concurrently abundant at similar levels. Conversely, heavy grazing of grasses and forbs that reduced height of herbaceous cover would be expected to reduce numbers of Mexican voles and accordingly numbers of mature females. Long-tailed voles would be predicted to decrease in abundance if useable forest habitat was saturated. Collectively, the envirograms, Table 2.23 and Figures 2.12–2.21 provide a means for designing manipulations that will further our understanding of factors that influence populations of these five small mammals in the Sacramento Mountains.

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Table 2.1. Temporal and spatial replication of small mammal abundance and microhabitat samples in the Sacramento Mountains, New Mexico (1991–1996). Asterisks indicate sites sampled also during fall of 1993 and winter and spring of 1994.

	Sites Sampled By Year [a]					
Habitat	1991	1992	1993	1994	1995	1996
Mid-seral	BLUF (0)	DELW (27)	DELW (60)*	DELW (34)	DELW (0)	DELW (0)
Mesic Forest	GRES (0)	HAYC (1)	HAYC (120)*	HAYC (0)	HAYC (0)	
		ZINK (0)	ZINK (90)	ZINK (30)	ZINK (0)	
		WAYL (5)	WAYL (51)	WAYL (65)		
		WIWH (27)	WIWH (80)	WIWH (14)		
		LWIL (38)	LWIL (83)			
Replicates:	2	6	6	5	3	1
Late Seral				GDSL (121)	GDSL (0)	GDSL (0)
Mesic Forest				SUNS (121)	SUNS (0)	
Replicates:	0	0	0	2	2	1
Montane		DELW (22)	DELW (29)*	DELW (54)	DELW (0)	DELW (0)
Meadow		HAYC (30)	HAYC (35)*	HAYC (40)	HAYC (0)	
		WILL (30)	WILL (0)	WILL (74)	WILL (0)	
		LWIL (27)	LWIL (0)	LWIL (78)		
		WAYL (19)	WAYL (32)	WAYL (54)		
		WIWH (28)	WIWH (0)	WIWH (76)		
Replicates:	0	6	6	6	3	1
Xeric Forest	$FIRE_1$ (0)	JAMS (19)	JAMS (94)*	JAMS (18)	JAMS (0)	JAMS (0)
	SIXT (0)	CARR (30)	CARR (19)	CARR (71)	CARR (0)	
		DRYB (31)	DRYB (40)	DRYB (48)	BRYB (0)	
		$FIRE_2$ (22)	$FIRE_2$ (99)*	$FIRE_2$ (0)		
		TRAL (3)	TRAL (118)	TRAL (0)		
		WALK (8)	WALK (102)	WALK (11)	WALK (0)	
Replicates:	2	6	6	6	4	1

[a] Number of trap stations where environmental variables were sampled is shown in parentheses. Site names and universal transverse mercator coordinates (zone 13) for center of trapping grid: BLUF–Bluff Springs (4303E, 36321N); CARR–Carr Gap (4547E, 36438N); DELW–Delworth (MF:4309E, 36330N; MM:4305E, 36324N); DRYB–Dry Burnt (4473E, 36458N); $FIRE_1$–Fire 1(4552E, 36450N); $FIRE_2$–Fire 2 (4547E, 36446N); GDSL–Goodsell (4322E, 36411N); GRES–Greasy Canyon (4418E 36328N); HAYC–Hay Canyon (MF:4396E, 36295N; MM:4393E, 36298N); JAMS–James Canyon (4447E, 36474N); LWIL–Lower Wills Canyon (MF:4338E, 36311N; MM:4331E, 36311N); SIXT–Sixteen Springs (4541E, 36491N); SUNS–Sunspot (4239E, 36288N); TRAL–Trail Canyon (4444E, 36215N); WALK–Walker (4521E, 36474N); WAYL–Wayland (MF:4375E, 36237N; MM:4375E, 36239N); WILL–Upper Wills Canyon(4304E, 36293N); WIWH–Willie White Canyon (MF:4322E, 36324N; MM:4313E, 36323N); ZINK–Zink Trick (4372E, 36513N).

Table 2.2. Attributes sampled at live-trapping stations to characterize habitat types and quantify microhabitat associations of five rodent species occurring in the Sacramento Mountains, New Mexico.

Variable	Sampling Method [a]	Description
SLOPE	PT	average between 2 slope (%) measurements using a clinometer
ELEV	PT	elevation to nearest 10 ft (converted to m) taken with an altimeter
HERBCAV	PI	% herbaceous cover averaged over 10 point-intercepts
SHRBCAV	PI	% shrub cover averaged over 10 point-intercepts
TREECAV	PI	% tree cover averaged over 10 point-intercepts
ROCKCAV	PI	% rock cover averaged over 10 point-intercepts
BARECAV	PI	% bare ground averaged over 10 point-intercepts
LITDPAV	PI	litter depth (cm) averaged over 10 point-intercepts
GFHTAV	PI	maximum grass/forb height (cm) averaged over 10 point-intercepts
SLOG1D and SLOG1V	FP	density (no./ha) and volume (m^3) of stage-1 logs (mid-diam. 10–30 cm)
SLOG2D and SLOG2V	FP	density (no./ha) and volume (m^3) of stage-2 logs (mid-diam. 10–30 cm)
SLOG3D and SLOG3V	FP	density (no./ha) and volume (m^3) of stage-3 logs (mid-diam. 10–30 cm)
SLOG4D and SLOG4V	FP	density (no./ha) and volume (m^3) of stage-4 logs (mid-diam. 10–30 cm)
LLOG1D and LLOG1V	FP	density (no./ha) and volume (m^3) of stage-1 logs (mid-diam. >30 cm)
LLOG2D and LLOG2V	FP	density (no./ha) and volume (m^3) of stage-2 logs (mid-diam. >30 cm)
LLOG3D and LLOG3V	FP	density (no./ha) and volume (m^3) of stage-3 logs (mid-diam. >30 cm)
LLOG4D and LLOG4V	FP	density (no./ha) and volume (m^3) of stage-4 logs (mid-diam. >30 cm)
LOG5TL	FP	total length (m) of stage-5 logs
SHRBD	FP	density (no. /ha) of shrubs (species specific) >0.5 m tall
CSAPLD	FP	density (no. /ha) of conifer saplings.
DSAPLD	FP	density (no. /ha) of deciduous saplings.
STUMPD	FP	density (no. /ha) of tree stumps.
LC20BA	VR	basal area (m^2 /ha) of live conifer trees using 20 BAF (species specific)
LH20BA	VR	basal area (m^2 /ha) of live deciduous trees using 20 BAF (species specific)
DC20BA	VR	basal area (m^2 /ha) of dead conifer trees using 20 BAF (species specific)
DH20BA	VR	basal area (m^2 /ha) of dead deciduous trees using 20 BAF (species specific)
LC20ST	VR	no. of stems of live conifer trees using 20 BAF (species; size specific)
LH20ST	VR	no. of stems of live deciduous trees using 20 BAF (species; size specific)
DC20ST	VR	no. of stems of dead conifer trees using 20 BAF (species; size specific)
DH20ST	VR	no. of stems of dead deciduous trees using 20 BAF (species; size specific)

[a] PT = point; PI = point-intercept; FP = fixed plot (78.5 m^2); VR = variable-radius plot.

Table 2.3. Linear models established *a priori* (original) and after initial analysis (exploratory) for predicting abundance (g/ha) of deer mice (DM) in the Sacramento Mountains, New Mexico during summers of 1992–1994. Regressor acronyms are defined in the text.

Model Set / Acronym	Model Structure (summer biomass of deer mice =)	Implied Effects
Original / DM_{Global}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet FWTEMP + \beta_5 \bullet MATFEM + \beta_6 \bullet COVER - \beta_7 \bullet INFCOMP$	Food supply, fall-winter temperatures, availability of mature females, cover from predation and the thermal environment, and interspecific interference competition influence summer biomass of deer mice..
DM_{C1}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet FWTEMP - \beta_5 \bullet INFCOMP$	Food supply and fal-winter temperatures, and interference competition.
DM_{C2}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet FWTEMP - \beta_5 \bullet DENDEP$	Food supply, fall-winter temperatures, and delayed density dependence.
DM_{C3}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet FWTEMP + \beta_5 \bullet MATFEM$	Food supply, fall-winter energy demand, and availability of mature females.
DM_{C4}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet COVER + \beta_5 \bullet ALTPREY$	Food supply, cover, and release from predation.
DM_{C5}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT - \beta_4 \bullet DENDEP + \beta_5 \bullet ALTPREY$	Food supply, delayed density dependence, and release from predation.
DM_{C6}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet MATFEM + \beta_4 \bullet COVER$	Food supply, availability of mature females, and cover.
DM_{C7}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet GFHT + \beta_3 \bullet COVER$	Microhabitat model.
DM_{C8}	$\beta_0 + \beta_1 \bullet MCONIF + \beta_2 \bullet PREVRAIN + \beta_3 \bullet FWTEMP$	Food supply and fall-winter temperatures.

Table 2.3. (Continued).

Model Set / Acronym	Model Structure (summer biomass of deer mice =)	Implied Effects
Exploratory /		
DM_{E1}	$\beta_0 + \beta_1 \bullet PREVRAIN + \beta_2 \bullet GFHT + \beta_3 \bullet FWTEMP$	Reduced model of food supply and fall-winter temperatures.
DM_{E2}	$\beta_0 + \beta_1 \bullet GFHT + \beta_2 \bullet FWTEMP + \beta_3 \bullet MATFEM$	Reduced model of food supply, fall-winter temperatures and availability of mature females.
DM_{E3}	$\beta_0 + \beta_1 \bullet PREVRAIN + \beta_2 \bullet FWTEMP + \beta_3 \bullet MATFEM$	Reduced model of food supply, fall-winter temperatures and availability of mature females.
DM_{E4}	$\beta_0 + \beta_1 \bullet PREVRAIN + \beta_2 \bullet FWTEMP$	Reduced model of food supply and fall-winter temperatures.
DM_{E5}	$\beta_0 + \beta_1 \bullet FWTEMP$	Fall-winter temperatures.
DM_{E6}	$\beta_0 + \beta_1 \bullet RSPRAIN + \beta_2 \bullet FWTEMP$	Food and water supply (indirect) and fall-winter temperatures.
DM_{E7}	$\beta_0 + \beta_1 \bullet MATFEM$	Availability of mature females.

Table 2.4. Linear models established *a priori* (original) and after initial analysis (exploratory) for predicting abundance (g/ha) of brush mice (BM) in the Sacramento Mountains, New Mexico during summers of 1992–1994. Regressor acronyms are defined in the text.

Model Set / Acronym	Model Structure (summer biomass of brush mice =)	Implied Effects
Original /		
BM_{Global}	$\beta_0 + \beta_1 \bullet PJTREE + \beta_2 \bullet PREVRAIN + \beta_3 \bullet SHRUBS + \beta_4 \bullet FWTEMP + \beta_5 \bullet MATFEM + \beta_6 \bullet ROCKS - \beta_7 \bullet INFCOMP$	Food supply, fall-winter temperatures, availability of mature females, cover from predation and thermal environment, and interspecific interference competition for den sites influence summer biomass of brush mice.
BM_{C1}	$\beta_0 + \beta_1 \bullet PJTREE + \beta_2 \bullet PREVRAIN + \beta_3 \bullet SHRUBS + \beta_4 \bullet ROCKS + \beta_5 \bullet LSCOV - \beta_6 \bullet INFCOMP$	Food[a] and presence of suitable den sites as modified by interference competition.
BM_{C2}	$\beta_0 + \beta_1 \bullet OAKS + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet ROCKS + \beta_5 \bullet LSCOV - \beta_6 \bullet INFCOMP$	Food[b] and presence of suitable den sites as modified by competition.
BM_{C3}	$\beta_0 + \beta_1 \bullet PJTREE + \beta_2 \bullet PREVRAIN + \beta_3 \bullet SHRUBS + \beta_4 \bullet RSPRAIN + \beta_5 \bullet FWTEMP$	Food[a] supply, water, and fall-winter temperatures.
BM_{C4}	$\beta_0 + \beta_1 \bullet OAKS + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet FWTEMP$	Food[b] supply and fall-winter temperatures..
BM_{C5}	$\beta_0 + \beta_1 \bullet PJTREE + \beta_2 \bullet PREVRAIN + \beta_3 \bullet SHRUBS + \beta_4 \bullet RSPRAIN + \beta_5 \bullet ROCKS + \beta_6 \bullet LSCOV$	Food[a], water, cover and den sites.
BM_{C6}	$\beta_0 + \beta_1 \bullet OAKS + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet ROCKS + \beta_5 \bullet LSCOV$	Food[b] supply, cover, and den sites.
BM_{C7}	$\beta_0 + \beta_1 \bullet PJTREE + \beta_2 \bullet PREVRAIN + \beta_3 \bullet SHRUBS + \beta_4 \bullet RSPRAIN + \beta_5 \bullet ROCKS + \beta_6 \bullet ALTPREY$	Food[a] supply, water, cover, and release from predation.
BM_{C8}	$\beta_0 + \beta_1 \bullet OAKS + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet ROCKS + \beta_5 \bullet LSCOV + \beta_6 \bullet ALTPREY$	Food[b] supply, cover, den sites and release from predation.
BM_{C9}	$\beta_0 + \beta_1 \bullet OAKS + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet ROCKS + \beta_5 \bullet ALTPREY$	Food[b] supply, cover, and release from predation.
BM_{C10}	$\beta_0 + \beta_1 \bullet PJTREE + \beta_2 \bullet PREVRAIN + \beta_3 \bullet RSPRAIN + \beta_4 \bullet MATFEM + \beta_5 \bullet ROCKS + \beta_6 \bullet LSCOV$	Food from conifers, water, availability of mature females, cover and dens.

Table 2.4. (Continued).

Model Set / Acronym	Model Structure (summer biomass of brush mice =)	Implied Effects
Original /		
BM_{C11}	$\beta_0 + \beta_1 \bullet OAKS + \beta_2 \bullet PREVRAIN + \beta_3 \bullet GFHT + \beta_4 \bullet MATFEM + \beta_5 \bullet ROCKS + \beta_6 \bullet LSCOV$	Food[b], water, availability of mature females, cover, and dens.
BM_{C12}	$\beta_0 + \beta_1 \bullet PJTREE + \beta_2 \bullet SHRUBS + \beta_3 \bullet ROCKS + \beta_4 \bullet LSCOV$	Microhabitat.
BM_{C13}	$\beta_0 + \beta_1 \bullet SHRUBS + \beta_2 \bullet MATFEM + \beta_3 \bullet ROCKS$	Food from shrubs, availability of females, and cover.
Exploratory /		
BM_{E1}	$\beta_0 + \beta_1 \bullet PREVRAIN + \beta_2 \bullet SHRUBS + \beta_3 \bullet MATFEM + \beta_4 \bullet ROCKS$	Food (shrub mast), availability of mature females, and cover.
BM_{E2}	$\beta_0 + \beta_1 \bullet PREVRAIN + \beta_2 \bullet OAKS + \beta_3 \bullet MATFEM + \beta_4 \bullet ROCKS$	Food (acorns), availability of mature females, and cover.
BM_{E3}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet ROCKS + \beta_3 \bullet INFCOMP$	Availability of mature females, cover, and interference competition for rock dens.
BM_{E4}	$\beta_0 + \beta_1 \bullet SHRUBS + \beta_2 \bullet MATFEM + \beta_3 \bullet ROCKS$	Food (shrub mast), availability of mature females, and cover.
BM_{E5}	$\beta_0 + \beta_1 \bullet OAKS + \beta_2 \bullet ROCKS$	Food (acorns) and cover; reduced microhabitat model.
BM_{E6}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet ROCKS$	Availability of mature females and cover.
BM_{E7}	$\beta_0 + \beta_1 \bullet MATFEM$	Availability of mature females.
BM_{E8}	$\beta_0 + \beta_1 \bullet ROCKS$	Rock cover.

[a] Food from conifer seeds, juniper berries, shrub mast, including acorns from low-growing oaks.

[b] Food as acorns from low-growing and tree oaks, and from grass or forb seeds and foliage.

Table 2.5. Linear models established *a priori* (original) and after initial analysis (exploratory) for predicting abundance (g/ha) of Mexican voles (MV) in the Sacramento Mountains, New Mexico during summers of 1992–1994. Regressor acronyms are defined in the text.

Model Set / Acronym	Model Structure (summer biomass of Mexican voles =)	Implied Effects
Original / MV_{Global}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet GFHT + \beta_3 \bullet RSPRAIN + \beta_4 \bullet MATFEM + \beta_5 \bullet INFCOMP + \beta_6 \bullet ALTPREY - \beta_7 \bullet DENSDEP$	Fall-winter temperatures, summer cover, food, and water supply, availability of sexually mature females, interspecific interference competition for meadow sites, release from predation, and delayed density-dependence influences summer abundance of Mexican voles.
MV_{C1}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet GFHT + \beta_3 \bullet RSPRAIN + \beta_4 \bullet MATFEM + \beta_5 \bullet ALTPREY - \beta_6 \bullet DENSDEP$	Fall-winter temperatures, cover, food, and water supply, availability of mature females, release from predation and delayed density-dependence.
MV_{C2}	$\beta_0 + \beta_1 \bullet GFHT + \beta_2 \bullet RSPRAIN + \beta_3 \bullet MATFEM - \beta_4 \bullet DENSDEP$	Summer cover, food, and water supply, availability of mature females, and delayed density-dependence.
MV_{C3}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet GFHT + \beta_3 \bullet RSPRAIN + \beta_4 \bullet ALTPREY$	Fall-winter temperatures, summer cover, food and water supply, and release from predation.
MV_{C4}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet GFHT + \beta_3 \bullet RSPRAIN$	Fall-winter temperature effects on energy demand, summer cover, food and water supply.
MV_{C5}	$\beta_0 + \beta_1 \bullet GFHT + \beta_2 \bullet RSPRAIN + \beta_3 \bullet MATFEM + \beta_4 \bullet INFCOMP$	Summer cover, food, and water supply, availability of mature females, effects of interference competition.
MV_{C6}	$\beta_0 + \beta_1 \bullet GFHT + \beta_2 \bullet RSPRAIN + \beta_3 \bullet MATFEM$	Summer cover, food, water supply, and availability of mature females.

Table 2.5. (Continued).

Model Set / Acronym	Model Structure (summer biomass of Mexican voles =)	Implied Effects
Original /		
MV_{C7}	$\beta_0 + \beta_1 \bullet GFHT + \beta_2 \bullet MATFEM + \beta_3 \bullet INFCOMP$	Summer cover and food supply, availability of mature females, and effects of interference competition.
MV_{C8}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet GFHT + \beta_3 \bullet ALTPREY$	Fall-winter temperatures, summer food and cover, and release from predation.
MV_{C9}	$\beta_0 + \beta_1 \bullet PSSRAIN + \beta_2 \bullet MATFEM + \beta_3 \bullet INFCOMP$	Previous summer-spring rain as an indirect effect on food and cover, availability of mature females, and effects of interference competition.
MV_{C10}	$\beta_0 + \beta_1 \bullet GFHT$	Summer food and cover; microhabitat effects model.
Exploratory /		
MV_{E1}	$\beta_0 + \beta_1 \bullet GFHT + \beta_2 \bullet MATFEM$	Summer food, cover, and availability of mature females.
MV_{E2}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet GFHT + \beta_3 \bullet MATFEM + \beta_4 \bullet INFCOMP$	Fall-winter temperatures, food, cover, availability of mature females, and interference competition.
MV_{E3}	$\beta_0 + \beta_1 \bullet GFHT + \beta_2 \bullet MATFEM - \beta_3 \bullet DENSDEP$	Summer food, cover, availability of mature females, and delayed density dependence.
MV_{E4}	$\beta_0 + \beta_1 \bullet GFHT\text{-}Q + \beta_2 \bullet MATFEM\text{-}Q + \beta_3 \bullet DENSDEP\text{-}Q$	Summer food, cover, availability of females and delayed density dependence (modeled as quadratic function).
MV_{E5}	$\beta_0 + \beta_1 \bullet MATFEM$	Availability of mature females.

Table 2.6. Linear models established *a priori* (original) and after initial analysis (exploratory) for predicting abundance (g/ha) of long-tailed voles (LV) in the Sacramento Mountains, New Mexico during summers of 1992–1994. Regressor acronyms are defined in the text.

Model Set / Acronym	Model Structure (summer biomass of long-tailed voles =)	Implied Effects
Original / LV_{Global}	$\beta_0 + \beta_1 \bullet$FWTEMP + $\beta_2 \bullet$SHRUBS + $\beta_3 \bullet$GFHT + $\beta_4 \bullet$MATFEM + $\beta_5 \bullet$LOGS + $\beta_6 \bullet$INFCOMP + $\beta_7 \bullet$ALTPREY	Fall-winter temperatures, food supply, cover, availability of sexually mature females, interspecific interference competition and release from predation influences summer biomass of long-tailed voles.
LV_{C1}	$\beta_0 + \beta_1 \bullet$FWTEMP + $\beta_2 \bullet$PSSRAIN + $\beta_3 \bullet$SHRUBS + $\beta_4 \bullet$GFHT + $\beta_5 \bullet$INFCOMP	Fall-winter temperatures, previous summer-spring rainfall, food supply, cover, and interference competition.
LV_{C2}	$\beta_0 + \beta_1 \bullet$FWTEMP + $\beta_2 \bullet$SHRUBS + $\beta_3 \bullet$GFHT + $\beta_4 \bullet$MATFEM + $\beta_5 \bullet$INFCOMP	Fall-winter temperatures, food supply, cover, availability of mature females, and interference competition.
LV_{C3}	$\beta_0 + \beta_1 \bullet$SHRUBS + $\beta_2 \bullet$GFHT + $\beta_3 \bullet$MATFEM − $\beta_4 \bullet$DENDEP	Food supply, cover, availability of mature females, and delayed density-dependence.
LV_{C4}	$\beta_0 + \beta_1 \bullet$SHRUBS-Q + $\beta_2 \bullet$GFHT-Q + $\beta_3 \bullet$MATFEM-Q − $\beta_4 \bullet$DENDEP-Q	Food supply, cover, availability of mature females, and delayed density-dependence (quadratic function).
LV_{C5}	$\beta_0 + \beta_1 \bullet$SHRUBS + $\beta_2 \bullet$GFHT + $\beta_3 \bullet$MATFEM + $\beta_4 \bullet$LOGS + $\beta_5 \bullet$ALTPREY	Food supply, cover including logs, availability of mature females, and release from predation.
LV_{C6}	$\beta_0 + \beta_1 \bullet$FWTEMP + $\beta_2 \bullet$GFHT + $\beta_3 \bullet$MATFEM + $\beta_4 \bullet$LOGS	Fall-winter temperatures, forb-grass supply, availability of mature females, and log cover.
LV_{C7}	$\beta_0 + \beta_1 \bullet$PSSRAIN + $\beta_2 \bullet$SHRUBS + $\beta_3 \bullet$LOGS	Previous summer-spring rainfall, food supply from shrubs, and log cover.

Table 2.6. (Continued).

Model Set / Acronym	Model Structure (summer biomass of long-tailed voles =)	Implied Effects
Original /		
LV_{C8}	$\beta_0 + \beta_1 \bullet$SHRUBS $+ \beta_2 \bullet$GFHT $+ \beta_3 \bullet$LOGS $+ \beta_4 \bullet$ALTPREY	Food supply, cover, and release from predation.
LV_{C9}	$\beta_0 + \beta_1 \bullet$SHRUBS-Q $+ \beta_2 \bullet$GFHT-Q $+ \beta_3 \bullet$LOGS-Q	Food supply, and log cover; microhabitat effects model (quadratic function).
LV_{C10}	$\beta_0 + \beta_1 \bullet$SHRUBS-Q $+ \beta_2 \bullet$RSPRAIN-Q $+ \beta_3 \bullet$LOGS-Q	Food from shrubs, extra water from recent spring rain, and log cover (quadratic function).
Exploratory /		
LV_{E1}	$\beta_0 + \beta_1 \bullet$FWTEMP $+ \beta_2 \bullet$GFHT $+ \beta_3 \bullet$MATFEM	Fall-winter temperatures, food and cover from forbs and grasses, and availability of mature females.
LV_{E2}	$\beta_0 + \beta_1 \bullet$FWTEMP $+ \beta_2 \bullet$GFHT $+ \beta_3 \bullet$MATFEM $+ \beta_4 \bullet$INFCOMP	Fall-winter temperatures, food, cover, availability of mature females, and interference competition.
LV_{E3}	$\beta_0 + \beta_1 \bullet$FWTEMP $+ \beta_2 \bullet$MATFEM $+ \beta_3 \bullet$INFCOMP	Fall-winter temperatures, availability of mature females, and interference competition.
LV_{E4}	$\beta_0 + \beta_1 \bullet$GFHT $+ \beta_2 \bullet$MATFEM $+ \beta_3 \bullet$INFCOMP	Food and cover from forbs and grasses, availability of females, and interference competition.
LV_{E5}	$\beta_0 + \beta_1 \bullet$MATFEM $+ \beta_2 \bullet$INFCOMP	Availability of mature females and interference competition.
LV_{E6}	$\beta_0 + \beta_1 \bullet$GFHT $+ \beta_2 \bullet$MATFEM	Food and cover from forbs and grasses, and availability of mature females.
LV_{E7}	$\beta_0 + \beta_1 \bullet$MATFEM	Availability of mature females.

Table 2.7. Linear models established *a priori* (original) and after initial analysis (exploratory) for predicting abundance (g/ha) of Mexican woodrats (MW) in the Sacramento Mountains, New Mexico during summers of 1992–1994. Regressor acronyms are defined in the text.

Model Set / Acronym	Model Structure (summer biomass of Mexican woodrats =)	Implied Effects
Original / MW_{Global}	$\beta_0 + \beta_1 \bullet CSAPL + \beta_2 \bullet SHRUBS - \beta_3 \bullet GFHT + \beta_4 \bullet MATFEM + \beta_5 \bullet ROCKS + \beta_6 \bullet LGLOG - \beta_7 \bullet DENDEP$	Food supply, availability of sexually mature females, cover, and delayed density-dependence influence summer biomass of Mexican woodrats..
MW_{C1}	$\beta_0 + \beta_1 \bullet SHRUBS - \beta_2 \bullet GFHT + \beta_3 \bullet MATFEM + \beta_4 \bullet ROCKS - \beta_5 \bullet DENDEP$	Food from shrubs and forbs, availability of mature females, cover, and delayed density-dependence.
MW_{C2}	$\beta_0 + \beta_1 \bullet MTMGOK - \beta_2 \bullet GFHT + \beta_3 \bullet MATFEM + \beta_4 \bullet ROCKS - \beta_5 \bullet DENDEP$	Food from mountain mahogony, Gambel oak, and forbs, availability of mature females, cover, and delayed density-dependence.
MW_{C3}	$\beta_0 + \beta_1 \bullet CSAPL + \beta_2 \bullet SHRUBS + \beta_3 \bullet MATFEM + \beta_4 \bullet ROCKS + \beta_5 \bullet ALTPREY$	Food from conifer CSAPLings and shrubs, availability of mature females, cover, and release from predation.
MW_{C4}	$\beta_0 + \beta_1 \bullet SHRUBS + \beta_2 \bullet MATFEM + \beta_3 \bullet ROCKS + \beta_4 \bullet LGLOG + \beta_5 \bullet ALTPREY$	Food from shrubs, availability of mature females, cover, and release from predation.
MW_{C5}	$\beta_0 + \beta_1 \bullet SHRUBS + \beta_2 \bullet MATFEM + \beta_3 \bullet ROCKS + \beta_4 \bullet LGLOG$	Food from shrubs, availability of mature females, and cover.
MW_{C6}	$\beta_0 + \beta_1 \bullet CSAPL + \beta_2 \bullet SHRUBS + \beta_3 \bullet RSPRAIN + \beta_4 \bullet ROCKS$	Food from conifer CSAPLings and shrubs, water from spring rains, and cover.
MW_{C7}	$\beta_0 + \beta_1 \bullet CSAPL + \beta_2 \bullet MTMGOK + \beta_3 \bullet RSPRAIN + \beta_4 \bullet ROCKS$	Food from conifer CSAPLings and mountain mahogany and Gambel oak, water from spring rains, and cover.

Table 2.7. (Continued).

Model Set / Acronym	Model Structure (summer biomass of Mexican woodrats =)	Implied Effects
Original /		
MW_{C8}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet CSAPL + \beta_3 \bullet SHRUBS - \beta_4 \bullet GFHT + \beta_5 \bullet ROCKS$	Fall-winter temperature, food supply, and cover.
MW_{C9}	$\beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet SHRUBS + \beta_3 \bullet RSPRAIN + \beta_4 \bullet ROCKS + \beta_5 \bullet LGLOG$	Fall-winter temperature, food from shrubs, water from spring rains, and cover.
MW_{C10}	$\beta_0 + \beta_1 \bullet MTMGOK + \beta_2 \bullet MATFEM + \beta_3 \bullet ROCKS + \beta_4 \bullet LGLOG$	Food from mountain mahogany and Gambel oak, availability of mature females, and cover.
MW_{C11}	$\beta_0 + \beta_1 \bullet CSAPL + \beta_2 \bullet SHRUBS - \beta_3 \bullet GFHT + \beta_4 \bullet ROCKS + \beta_5 \bullet LGLOG$	Food supply and cover; microhabitat effects model.
Exploratory /		
MW_{E1}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet ROCKS + \beta_3 \bullet LGLOG$	Availability of mature females, rock cover, and large log cover.
MW_{E2}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet RSPRAIN + \beta_3 \bullet ROCKS + \beta_4 \bullet LGLOG$	Availability of mature females, moisture from recent spring rains, rock cover and large log cover.
MW_{E3}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet RSPRAIN + \beta_3 \bullet LGLOG$	Availability of mature females, moisture from recent spring rains, and large log cover.
MW_{E4}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet ROCKS$	Availability of females, and rock cover.
MW_{E5}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet LGLOG$	Availability of mature females and large log cover
MW_{E6}	$\beta_0 + \beta_1 \bullet MATFEM + \beta_2 \bullet RSPRAIN$	Availability of mature females and moisture from recent spring rains.
MW_{E7}	$\beta_0 + \beta_1 \bullet MATFEM$	Availability of mature females.

Table 2.8. Mean summer density ($\hat{N}$/ha), mass (g), and biomass ($\hat{\bar{B}}_{ik}$; g/ha) of five murid rodents occurring in three habitats (mesic forest, montane meadow, and xeric forest) of the Sacramento Mountains, New Mexico (1991–1996).

Species (i)	Habitat (k) [a]	$\overline{Density}$ ($\hat{N}$/ha)	$\overline{mass}$ (g)	$\hat{\bar{B}}_{ik}$ (g/ha)	$\overline{SE}$ [b] (g/ha)	CV_e [c] (%)	n_1, n_2, $\bar{n}$ [d]
Deer mouse	Mesic Forest-L	7.8	15.2	125.5	10.79	9	5, 5, 39
	Mesic Forest-M	10.6	17.4	175.7	8.78	5	23, 23, 45
	Montane Meadow	8.4	18.8	157.5	13.45	9	22, 21, 20
	Xeric Forest	4.9	17.4	84.6	6.18	7	25, 24, 25
Brush mouse	Mesic Forest-L	0.1	20.0	1.0	—	—	5, 0, 1
	Mesic Forest-M	0.3	23.8	8.1	13.21	209	23, 3, 2
	Xeric Forest	5.8	23.6	138.6	7.22	5	25, 21, 29
Mexican vole	Mesic Forest-L	0.4	27.5	10.3	15.33	149	5, 1, 2
	Mesic Forest-M	1.4	25.6	38.8	39.36	101	23, 4, 4
	Montane Meadow	59.8	28.4	1739.7	71.61	4	22, 20, 85
	Xeric Forest	1.5	23.3	38.0	9.65	25	25, 7, 7
Long-tailed vole	Mesic Forest-L	3.3	31.2	104.1	14.32	14	5, 4, 15
	Mesic Forest-M	6.4	33.3	213.5	38.01	18	23, 15, 20
	Montane Meadow	11.2	34.9	373.0	70.23	19	22, 17, 18
	Xeric Forest	< 0.1	33.0	0.7	—	—	25, 0, 1
Mexican woodrat	Mesic Forest-L	0.7	122.4	81.2	28.36	35	5, 3, 5
	Mesic Forest-M	0.9	120.2	106.1	17.12	16	23, 16, 6
	Montane Meadow	0.2	113.9	28.9	53.88	187	22, 2, 2
	Xeric Forest	1.1	119.6	132.7	14.09	11	25, 21, 7

[a] For Mesic Forest, L = late seral stage (dominant conifers > 200 yrs old); M = mid-seral stage (dominant conifers 60–100 yrs old).

[b] The square root of the average enumeration error of $\hat{B}_i$ within each habitat or habitat seral stage.

[c] CV_e is the percent of variation in $\hat{\bar{B}}_{ik}$ attributed to enumeration error, relative to the magnitude of $\hat{\bar{B}}_{ik}$.

[d] n_1 is the number of replicates (sites and years) used to estimate mean density and mean biomass; n_2 is the number of replicates where enough captures permitted estimation of the sampling variance of biomass; $\bar{n}$ is the mean number of individuals captured and marked per replicate. Mean values of density and $\hat{B}_i$ include zero values for sites or years where a species was not captured except for brush mice which were never captured in montane meadows and were excluded.

Table 2.9. Temporal and spatial effects on summer biomass (g/ha) of five murid rodents occurring in three habitats (mid-seral mesic forest, montane meadow, and xeric forest) of the Sacramento Mountains, New Mexico (1992–1995).

		Deer mouse		Brush mouse		Mexican vole		Long-tailed vole		Mexican woodrat	
Effect [a]	d.f. [b]	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Habitat	2, 7	1.00	0.414	7.29	0.019	4.40	0.058	2.48	0.154	28.04	0.001
Year	3, 7	9.74	0.007	21.57	0.007	7.91	0.012	5.14	0.034	4.01	0.059
Habitat x Year	6, 7	1.75	0.241	17.38	0.007	7.50	0.009	4.27	0.039	0.94	0.522

[a] The effects were quantified as *F*-ratios between variances estimated with a mixed model of repeated measures of biomass over time and assuming unstructured covariances.

[b] Numerator and denominator degrees of freedom.

Table 2.10. Mean biomass (g/ha) of five murid rodents occurring in mid-seral mesic forests and xeric forests of the Sacramento Mountains, New Mexico during July–August 1991 and 1992.

Species / habitat	[illegible] 1991	[illegible] 1992	[illegible] 1991	[illegible] 1992	n_1 [b] 1991	n_1 [b] 1992	n_2 1991	n_2 1992	Z [c]	P
Deer mouse										
mid-seral mesic forest	783	85	47.1	10.6	2	6	169	23	14.44	<0.001
xeric forest	89	110	33.4	8.3	2	6	24	33	0.61	0.541
Brush mouse										
mid-seral mesic forest	58	1	19.4	31.5	1	1	12	1	1.56	0.119
xeric forest	44	240	14.6	16.5	1	5	10	45	8.93	<0.001
Mexican vole										
mid-seral mesic forest	95	104	66.4	47.6	1	3	5	7	0.11	0.915
xeric forest	74	121	30.2	13.6	1	4	8	19	1.41	0.158
Long-tailed vole										
mid-seral mesic forest	432	516	191.2	103.4	2	4	16	49	0.39	0.700
Mexican woodrat										
mid-seral mesic forest	55	146	97.8	40.3	1	5	2	5	0.86	0.387
xeric forest	69	185	14.3	28.0	1	6	4	9	3.67	<0.001

[a] Square root of the enumeration variance averaged across site replicates.

[b] n_1 = number of sites where enough animals were captured and marked to estimate enumeration error; n_2 = mean number of marked animals used to estimate biomass at a given site.

[c] Z tests H_o: no difference in biomass between 1991 and 1992 within a habitat.

Table 2.11. Biomass (g/ha) of five murid rodents occurring at a mid- and one late-seral mesic forest site, one montane meadow site, and one xeric forest site in the Sacramento Mountains, New Mexico during July–August 1995 and 1996.

	[illegible]		[illegible]		n [a]					
Species / seral stage	1995	1996	1995	1996	1995	1996	Z_1 [b]	P_1	Z_2 [c]	P_2
Deer mouse										
late-seral mesic forest	52	182	13.8	27.5	22	52	4.24	<0.001	1.72	0.086
mid-seral mesic forest	96	260	15.4	36.0	34	72	4.19	<0.001		
montane meadow	204	305	48.1	55.3	19	42	1.38	0.167		
xeric forest	53	183	9.9	37.0	22	49	3.41	0.001		
Brush mouse										
xeric forest	11	71	2.9	16.5	3	19	3.56	<0.001		
Mexican vole										
montane meadow	4184	2331	338.1	353.1	244	107	3.79	<0.001		
Long-tailed vole										
late-seral mesic forest	36	390	17.2	51.6	5	52	6.53	<0.001	2.19	0.028
mid-seral mesic forest	48	241	15.4	44.3	7	27	4.12	<0.001		
Mexican woodrat										
late-seral mesic forest	80	239	58.2	47.5	4	11	2.13	0.034	1.70	0.088
mid-seral mesic forest	84	113	57.0	57.0	3	5	0.35	0.725		
xeric forest	87	212	33.9	47.2	5	11	2.15	0.032		

[a] Number of marked animals used to estimate biomass.

[b] Z_1 tests H_o: no difference in biomass between 1995 and 1996 within a seral stage or habitat.

[c] Z_2 tests H_o: no difference in biomass between mesic forest seral stages in 1996.

Table 2.12. Seral-stage and year effects on biomass (g/ha) of three rodents occurring in mid- (60–100 yr) and late (>200 yr) seral stages of mesic forest of the Sacramento Mountains, New Mexico during July–August 1994 and 1995.

		Deer Mouse		Long-tailed vole		Mexican woodrat	
Effect [a]	df [b]	*F*	*P*	*F*	*P*	*F*	*P*
Seral stage	1, 3	1.99	0.253	0.20	0.688	1.78	0.274
Year	1, 3	27.59	0.013 *	0.12	0.752	0.53	0.514
Stage x Year	1, 3	0.65	0.478	<0.01	0.952	0.84	0.428

[a] Effects were tested using a repeated measures, mixed model assuming unstructured covariances.

[b] Numerator, denominator (mid seral = 3 sites; late seral = 2 sites).

* Significant at the $\alpha = 0.05$ level.

Table 2.13. Coefficients of modeled effects on summer abundance (g/ha) of deer mice in the Sacramento Mountains, New Mexico (1992–1994) and weights of model reliability. Sample size (n = 42) is based on 20 sites each sampled during 1, 2 or 3 summers. Model order based on ΔAIC_c. Regressor variables are described in the text and Table 2.3.

DM[a]		R^2	Original Models[c]		All Models[d]				PREV-			MAT-	
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	INTERCEPT	MCONIF	RAIN	GFHT	FWTEMP	FEM	COVER
E2	5	53.5	–	–	0	0.6701*	−127.768	–	–	2.226	−26.267	8.214	–
E3	5	49.1	–	–	3.73	0.1037*	−55.668	–	−1.779	–	−39.219	7.272	–
Global	9	61.5	0	0.4822*	3.95	0.0931*	22.258	−0.146	−2.509	−2.948	−35.900	8.110	−0.0012
C3	7	55.0	0.20	0.4355*	4.15	0.0841*	−121.657	−0.500	−0.549	1.584	−34.625	8.188	–
E7	3	39.2	–	–	6.17	0.0306	50.617	–	–	–	–	9.479	–
C6	6	47.8	3.59	0.0800*	7.54	0.0155	−195.406	−0.598	3.824	–	–	9.591	−0.0029
E5	3	29.3	–	–	12.51	0.0013	−218.138	–	–	–	−52.350	–	–
E6	4	30.3	–	–	14.34	0.0005	−201.316	–	–	–	−45.742	–	–
E4	4	30.1	–	–	14.46	0.0005	−90.604	–	−2.568	–	−61.323	–	–
C8	5	32.1	11.89	0.0013	15.84	0.0002	−181.098	−0.556	−1.171	–	−62.167	–	–
E1	5	31.3	–	–	16.31	0.0002	−82.965	–	−2.656	1.100	−59.540	–	–
C1	7	39.8	12.45	0.0010	16.39	0.0002	−46.978	−0.138	−3.145	−4.206	−63.095	–	–
C2	7	33.7	16.50	0.0001	20.45	<0.0001	−209.643	−0.408	−0.684	0.602	−60.822	–	–
C7	5	7.1	25.04	<0.0001	28.98	<0.0001	91.401	0.506	–	2.052	–	–	−0.0022
C5	7	16.3	26.31	<0.0001	30.26	<0.0001	−472.962	−0.374	8.308	2.183	–	–	–
C4	7	14.5	27.19	<0.0001	31.14	<0.0001	−404.523	−0.397	7.292	2.003	–	–	−0.0004

Table 2.13. (Continued).

DM[a]		R^2	Original Models[c]		All Models[d]					
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	INFCOMP	ALTPREY	DENDEP	SPRRAIN
E2	5	53.5	–	–	0	0.6701*	–	–	–	–
E3	5	49.1	–	–	3.73	0.1037*	–	–	–	–
Global	9	61.5	0	0.4822*	3.95	0.0931*	0.879	–	–	–
C3	7	55.0	0.20	0.4355*	4.15	0.0841*	–	–	–	–
E7	3	39.2	–	–	6.17	0.0306	–	–	–	–
C6	6	47.8	3.59	0.0800*	7.54	0.0155	–	–	–	–
E5	3	29.3	–	–	12.51	0.0013	–	–	–	–
E6	4	30.3	–	–	14.34	0.0005	–	–	–	2.244
E4	4	30.1	–	–	14.46	0.0005	–	–	–	–
C8	5	32.1	11.89	0.0013	15.84	0.0002	–	–	–	–
E1	5	31.3	–	–	16.31	0.0002	–	–	–	–
C1	7	39.8	12.45	0.0010	16.39	0.0002	0.955	–	–	–
C2	7	33.7	16.50	0.0001	20.45	<0.0001	–	–	−0.848	–
C7	5	7.1	25.04	<0.0001	28.98	<0.0001	–	–	–	–
C5	7	16.3	26.31	<0.0001	30.26	<0.0001	–	−0.009	−0.949	–
C4	7	14.5	27.19	<0.0001	31.14	<0.0001	–	−0.009	–	–

[a] Linear regression models of deer mouse abundance described in Table 2.3.

[b] Number of model parameters estimated from data including intercept coefficient, effect coefficients, and a residual error term.

[c] Weighted according to minimum AIC_c value of the nine *a priori* models.

[d] Weighted according to minimum AIC_c value of the nine *a priori* and seven exploratory models.

Table 2.14. Precision and relative importance of ecological factors associated with summer abundance (g/ha) of deer mice in the Sacramento Mountains, New Mexico (1992–1994). Two sets of regression coefficients ($\bar{\beta}$) are given; those averaged over *a priori* (original) models and the other averaged over original and exploratory (all) models. CVs of the average coefficients include variation associated with uncertainty of model structure. Relative importance (RI) of each regressor variable is also shown for both model sets and is based on the sums of Akaike weights for each model that included the regressor. Asterisks indicate effects included in the 95% confidence set of models. Regressor acronyms are defined in the text. Factors are ordered from highest to lowest according to RI in the original model set.

	Original Models			All Models		
Factor	$\bar{\beta}$	CV(%)	RI	$\bar{\beta}$	CV(%)	RI
MCONIF	−0.337	164.1	1.000*	−0.065	181.4	0.193*
PREVRAIN	−1.147	329.7	1.000*	−0.408	274.1	0.297*
MATFEM	8.243	23.3	0.998*	8.141	23.7	0.997*
FWTEMP	−32.535	47.5	0.920*	−28.083	48.7	0.954*
GFHT	−0.736	366.9	0.919*	1.349	113.2	0.848*
COVER	−0.0008	189.2	0.562*	−0.0002	203.8	0.109*
INFCOMP	0.425	66.7	0.483*	0.082	100.0	0.093*
DENDEP	−0.0001	151.1	0.000	−0.00002	151.1	0.000
ALTPREY	≈0.[a]	163.2	0.000	≈0.[a]	163.2	0.000
RSPRAIN	–	–	–	0.001	165.4	0.001

[a] ≤0.000001

Table 2.15. Coefficients of modeled effects on summer abundance (g/ha) of brush mice in the Sacramento Mountains, New Mexico (1992–1994) and weights of model reliability. Sample size (n = 42) is based on 20 sites each sampled during 1, 2 or 3 summers. Model order based on ΔAIC_c. Regressor variables are described in the text and Table 2.4.

BM[a]		R^2	Original Models[c]		All Models[d]		INTER-		PREV-	FW-	RSP-		
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	CEPT	PJTREE	RAIN	TEMP	RAIN	SHRUBS	GFHT
E4	5	93.5	–	–	0	0.3414*	10.159	–	–	–	–	–	–
E7	3	92.6	–	–	0.33	0.2902*	3.942	–	–	–	–	–	–
E6	4	92.8	–	–	1.81	0.1382*	−6.326	–	–	–	–	–	–
E2	6	93.5	–	–	2.66	0.0902*	−32.300	–	0.572	–	–	–	–
E3	5	93.0	–	–	2.93	0.0789*	−9.804	–	–	–	–	–	–
C13	5	92.8	0	0.8547*	4.35	0.0389*	−6.161	–	–	–	–	0.0004	–
E1	6	92.9	–	–	6.17	0.0156	134.993	–	−1.842	–	–	0.0007	–
C11	8	93.5	4.19	0.1052*	8.53	0.0048	−17.350	–	0.425	–	–	–	−0.202
C10	8	93.1	6.95	0.0265	11.29	0.0012	156.736	0.043	−2.193	–	0.430	–	–
Global	9	93.4	8.28	0.0136	12.63	0.0006	180.819	0.038	−2.570	−1.406	–	0.0012	–
E5	4	63.4	–	–	69.95	<0.0001	−48.780	–	–	–	–	–	–
E8	3	58.5	–	–	72.85	<0.0001	−99.384	–	–	–	–	–	–
C2	8	67.9	71.45	<0.0001	75.80	<0.0001	100.102	–	−2.352	–	–	–	1.087
C1	8	67.7	71.73	<0.0001	76.07	<0.0001	440.910	−0.173	−7.075	–	–	0.0026	–
C4	6	62.6	71.85	<0.0001	76.20	<0.0001	37.629	–	−1.255	−4.879	–	–	0.144
C6	7	63.9	73.32	<0.0001	77.67	<0.0001	1.189	–	−1.027	–	–	–	1.190
C9	7	63.8	73.41	<0.0001	77.76	<0.0001	−40.501	–	−0.352	–	–	–	0.878
C12	6	60.5	74.15	<0.0001	78.49	<0.0001	−91.703	−0.132	–	–	–	0.0024	–
C7	8	64.8	75.30	<0.0001	79.64	<0.0001	368.095	−0.126	−7.061	–	4.570	0.0019	–
C5	8	64.6	75.52	<0.0001	79.87	<0.0001	442.653	−0.137	−7.981	–	4.601	0.0004	–
C8	8	63.9	76.37	<0.0001	80.72	<0.0001	4.208	–	−1.100	–	–	–	1.084
C3	7	57.8	79.82	<0.0001	84.16	<0.0001	999.615	0.077	−11.740	35.237	7.592	0.0091	–

Table 2.15. (Continued).

BM[a] Model	K[b]	R^2 (%)	Original Models[c] ΔAIC_c	Original Models[c] Weight	All Models[d] ΔAIC_c	All Models[d] Weight	OAKS	MAT-FEM	ROCKS	LSCOV	INF-COMP	ALT-PREY
E4	5	93.5	–	–	0	0.3414*	0.011	16.058	−0.779	–	–	–
E7	3	92.6	–	–	0.33	0.2902*	–	17.547	–	–	–	–
E6	4	92.8	–	–	1.81	0.1382*	–	16.654	0.432	–	–	–
E2	6	93.5	–	–	2.66	0.0902*	0.012	16.076	−0.790	–	–	–
E3	5	93.0	–	–	2.93	0.0789*	–	16.313	0.408	–	7.112	–
C13	5	92.8	0	0.8547*	4.35	0.0389*	–	16.646	0.388	–	–	–
E1	6	92.9	–	–	6.17	0.0156	–	16.432	0.077	–	–	–
C11	8	93.5	4.19	0.1052*	8.53	0.0048	0.012	16.119	−0.891	−0.0003	–	–
C10	8	93.1	6.95	0.0265	11.29	0.0012	–	16.635	−0.152	0.0168	–	–
Global	9	93.4	8.28	0.0136	12.63	0.0006	–	16.197	−0.361	–	7.912	–
E5	4	63.4	–	–	69.95	<0.0001	0.027	–	1.640	–	–	–
E8	3	58.5	–	–	72.85	<0.0001	–	–	5.165	–	–	–
C2	8	67.9	71.45	<0.0001	75.80	<0.0001	0.022	–	1.583	0.0060	28.436	–
C1	8	67.7	71.73	<0.0001	76.07	<0.0001	–	–	3.854	−0.0574	35.555	–
C4	6	62.6	71.85	<0.0001	76.20	<0.0001	0.037	–	–	–	–	–
C6	7	63.9	73.32	<0.0001	77.67	<0.0001	0.024	–	2.174	0.0246	–	–
C9	7	63.8	73.41	<0.0001	77.76	<0.0001	0.025	–	2.096	–	–	0.0005
C12	6	60.5	74.15	<0.0001	78.49	<0.0001	–	–	5.482	−0.0712	–	–
C7	8	64.8	75.30	<0.0001	79.64	<0.0001	–	–	4.800	–	–	0.0045
C5	8	64.6	75.52	<0.0001	79.87	<0.0001	–	–	4.751	0.0274	–	–
C8	8	63.9	76.37	<0.0001	80.72	<0.0001	0.024	–	2.197	0.0278	–	0.0014
C3	7	57.8	79.82	<0.0001	84.16	<0.0001	–	–	–	–	–	–

[a] Linear regression models of brush mouse abundance described in Table 2.4.

[b] Number of model parameters estimated from data, including intercept coefficient, effect coefficients, and a residual error term.

[c] Weighted according to minimum AIC_c value of the 14 *a priori* models.

[d] Weighted according to minimum AIC_c value of the 14 *a priori* and eight exploratory models.

Table 2.16. Precision and relative importance of ecological factors associated with summer abundance (g/ha) of brush mice in the Sacramento Mountains, New Mexico (1992–1994). Two sets of regression coefficients ($\bar{\beta}$) are given; those averaged over *a priori* (original) models and the other averaged over original and exploratory (all) models. CVs of the average coefficients include variation associated with uncertainty of model structure. Relative importance (RI) of each regressor variable is also shown for both model sets and is based on the sums of Akaike weights for each model that included the regressor. Asterisks indicate effects included in the 95% confidence set of models. Regressor acronyms are defined in the text. Factors are ordered from highest to lowest according to RI in the original model set.

	Original Models			All Models		
Factor	$\bar{\beta}$	CV(%)	RI	$\bar{\beta}$	CV(%)	RI
MATFEM	16.584	6.8	1.000*	16.624	7.3	1.000*
ROCKS	0.229	354.6	1.000*	−0.234	299.6	0.710*
SHRUBS	0.0003	11,095.0	0.868*	0.00002	9,020.6	0.055
PREVRAIN	−0.048	595.4	0.145*	0.020	945.1	0.112*
LSCOV	0.0004	6,168.9	0.132*	0.00002	6,169.1	0.006
GFHT	−0.021	458.8	0.105*	−0.001	460.9	0.005
OAKS	0.001	699.3	0.105*	0.005	681.8	0.436*
PJTREE	0.002	581.9	0.040	0.00008	582.5	0.002
RSPRAIN	0.011	283.0	0.026	0.0005	283.9	0.001
INFCOMP	0.107	103.9	0.014	0.566	98.4	0.080*
FWTEMP	−0.019	239.8	0.014	−0.0009	240.3	0.001
ALTPREY	≈0.[a]	6,420.0	0.000	≈0.[a]	6,420.0	0.000

[a] ≤0.000001

Table 2.17. Coefficients of modeled effects on summer abundance (g/ha) of Mexican voles in the Sacramento Mountains, New Mexico (1992–1994) and weights of model reliability. Sample size (n = 42) is based on 20 sites each sampled during 1, 2 or 3 summers. Model order based on ΔAIC_c. Regressor variables are described in the text and Table 2.5.

MV[a]		R^2	Original Models[c]		All Models[d]		INTER-	FW-		RSP-	MAT-	INF-
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	CEPT	TEMP	GFHT	RAIN	FEM	COMP
Global	9	95.5	0	0.9202*	0	0.9051*	86.524	68.514	76.759	−3.073	46.708	35.466
C7	5	93.2	5.55	0.0573*	5.52	0.0563*	−449.116	–	70.484	–	35.714	31.787
C5	6	93.4	7.43	0.0224	7.39	0.0221	−563.997	–	65.872	13.628	37.300	30.017
E2	6	93.3	–	–	8.01	0.0162	−246.431	33.087	71.222	–	35.375	32.443
E3	5	91.2	–	–	16.45	0.0002	−423.390	–	89.776	–	54.277	–
C2	6	91.3	18.60	0.0001	18.57	0.0001	−543.283	–	83.830	13.857	54.065	–
C1	8	92.3	19.62	<0.0001	19.51	<0.0001	−323.223	61.391	81.530	15.015	60.016	–
C6	5	89.7	23.00	<0.0001	22.96	<0.0001	−748.100	–	72.470	34.854	42.698	–
E1	4	88.7	–	–	24.23	<0.0001	−455.142	–	86.554	–	39.126	–
C9	5	88.7	26.92	<0.0001	26.88	<0.0001	−376.176	–	–	–	65.920	37.638
C10	3	83.7	37.42	<0.0001	37.38	<0.0001	−685.259	–	149.040	–	–	–
E4	5	84.3	–	–	14.83	<0.0001	−34.137	–	–	–	–	–
C4	5	84.0	41.63	<0.0001	41.59	<0.0001	−627.210	42.357	144.435	22.567	–	–
C8	5	83.7	42.42	<0.0001	42.38	<0.0001	−788.130	−15.134	148.665	–	–	–
E5	3	81.5	–	–	42.60	<0.0001	−17.029	–	–	–	79.436	–
C3	6	84.0	44.34	<0.0001	44.30	<0.0001	−632.796	43.965	144.303	22.744	–	–

Table 2.17. (Continued).

MV[a] Model	K[b]	R^2 (%)	Original Models[c] ΔAIC_c	Original Models[c] Weight	All Models[d] ΔAIC_c	All Models[d] Weight	ALT-PREY	DENDEP	PSS-RAIN	GFHT_Q	MAT-FEM_Q	DEND_Q
Global	9	95.5	0	0.9202*	0	0.9051*	−0.121	−6.594	–	–	–	–
C7	5	93.2	5.55	0.0572*	5.55	0.0563*	–	–	–	–	–	–
C5	6	93.4	7.43	0.0224	7.43	0.0221	–	–	–	–	–	–
E2	6	93.3	–	–	8.05	0.0162	–	–	–	–	–	–
E3	5	91.2	–	–	16.48	0.0002	–	−7.635	–	–	–	–
C2	6	91.3	18.60	0.0001	18.60	0.0001	–	−6.812	–	–	–	–
C1	8	92.3	19.62	<0.0001	19.62	<0.0001	0.302	−8.965	–	–	–	–
C6	5	89.7	23.00	<0.0001	23.00	<0.0001	–	–	–	–	–	–
E1	4	88.7	–	–	24.27	<0.0001	–	–	–	–	–	–
C9	5	88.7	26.92	<0.0001	26.92	<0.0001	–	–	4.848	–	–	–
C10	3	83.7	37.42	<0.0001	37.42	<0.0001	–	–	–	–	–	–
E4	5	84.3	–	–	40.80	<0.0001	–	–	–	6.856	0.839	0.026
C4	5	84.0	41.63	<0.0001	41.63	<0.0001	–	–	–	–	–	–
C8	5	83.7	42.42	<0.0001	42.42	<0.0001	0.017	–	–	–	–	–
E5	3	81.5	–	–	42.64	<0.0001	–	–	–	–	–	–
C3	6	84.0	44.34	<0.0001	44.34	<0.0001	0.025	–	–	–	–	–

[a] Linear regression models of Mexican vole abundance described in Table 2.5.

[b] Number of model parameters estimated from data including intercept coefficient, effect coefficients, and a residual error term.

[c] Weighted according to minimum AIC_c value of the 11 *a priori* models.

[d] Weighted according to minimum AIC_c value of the 11 *a priori* and five exploratory models.

Table 2.18 Precision and relative importance of ecological factors associated with summer abundance (g/ha) of Mexican voles in the Sacramento Mountains, New Mexico (1992–1994). Two sets of regression coefficients ($\bar{\beta}$) are given; those averaged over *a priori* (original) models and the other averaged over original and exploratory (all) models. CVs of the average coefficients include variation associated with uncertainty of model structure. Relative importance (RI) of each regressor variable is also shown for both model sets and is based on the sums of Akaike weights for each model that included the regressor. Asterisks indicate effects included in the 95% confidence set of models. Regressor acronyms are defined in the text. Factors are ordered from highest to lowest according to RI in the original model set.

	Original Models			All Models		
Factor	$\bar{\beta}$	CV(%)	RI	$\bar{\beta}$	CV(%)	RI
GFHT	76.156	17.7	1.000*	76.080	17.8	1.000*
MATFEM	45.869	18.3	1.000*	45.701	18.5	1.000*
INFCOMP	35.128	20.5	1.000*	35.076	20.5	1.000*
RSPRAIN	−2.520	636.9	0.943*	−2.478	636.9	0.927*
DENDEP	−6.069	34.1	0.920*	−5.970	34.4	0.905*
FWTEMP	63.048	104.3	0.920*	62.548	105.5	0.921*
ALTPREY	−0.111	118.3	0.920*	−0.110	118.4	0.905*
PSSRAIN	0.000006	279.4	0.000	0.000006	279.4	0.000
GFHT_Q	–	–	–	≈0.[a]	100.8	0.000
MATFEM_Q	–	–	–	≈0.[a]	103.6	0.000
DEND_Q	–	–	–	≈0.[a]	127.3	0.000

[a] ≤0.000001

Table 2.19. Coefficients of modeled effects on summer abundance (g/ha) of long-tailed voles in the Sacramento Mountains, New Mexico (1992–1994) and weights of model reliability. Sample size (n = 42) is based on 20 sites each sampled during 1, 2 or 3 summers. Model order based on ΔAIC_c. Regressor variables are described in the text and Table 2.6.

LV[a]		R^2	Original Models[c]		All Models[d]		INTER-	FW-			MAT-		INF-	ALT-
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	CEPT	TEMP	SHRUBS	GFHT	FEM	LOGS	COMP	PREY
E4	5	79.7	–	–	0	0.6172*	114.612	–	–	−26.193	35.014	–	8.908	–
E2	6	80.3	–	–	1.52	0.2883*	−98.388	−34.764	–	−26.723	34.093	–	8.911	–
C2	7	80.3	0	0.7190*	4.41	0.0680*	−93.142	−34.394	−0.0006	−26.842	34.043	–	8.914	–
Global	9	82.3	1.88	0.2810*	6.29	0.0266	−209.982	−58.583	0.0059	−24.397	38.155	−0.402	8.593	−0.030
E6	4	61.7	–	–	24.14	<0.0001	−82.765	–	–	16.457	37.878	–	–	–
E1	5	62.3	–	–	26.10	<0.0001	−293.856	−34.442	–	15.939	36.966	–	–	–
C6	6	64.2	22.22	<0.0001	26.64	<0.0001	−406.730	−63.980	–	12.470	39.301	−0.396	–	–
C3	6	63.1	23.49	<0.0001	27.91	<0.0001	−105.570	–	0.0007	16.130	32.941	–	4.377	–
E5	4	57.1	–	–	28.97	<0.0001	−22.333	–	–	–	35.072	–	–	–
C5	7	64.2	25.12	<0.0001	29.53	<0.0001	−37.181	–	0.0033	19.394	42.188	−0.342	4.305	–
E3	5	58.8	–	–	29.83	<0.0001	−194.292	−27.701	–	–	34.339	–	–	–
E7	3	48.8	–	–	33.91	<0.0001	−50.938	–	–	–	42.997	–	9.096	–
C1	7	58.3	31.51	<0.0001	35.92	<0.0001	−858.922	−51.253	−0.0055	−27.171	–	–	–	–
C4	6	44.8	40.40	<0.0001	44.81	<0.0001	−65.932	–	0.0102	2.602	33.389	–	–	−0.048
C7	5	34.7	44.77	<0.0001	49.18	<0.0001	56.854	–	−0.0121	–	–	−0.288	–	–
C8	6	28.9	51.06	<0.0001	55.47	<0.0001	−633.475	–	−0.0177	21.646	–	0.347	–	−0.003
C10	5	22.2	52.10	<0.0001	56.51	<0.0001	−1.541	–	−0.0100	–	–	–	–	–
C9	5	17.9	54.38	<0.0001	58.79	<0.0001	−633.475	–	−0.0414	19.732	–	0.241	–	–

Table 2.19. (Continued).

LV[a] Model	K[b]	R^2 (%)	Original Models[c] ΔAIC_c	Original Models[c] Weight	All Models[d] ΔAIC_c	All Models[d] Weight	PSS-RAIN	DEN-DEP	GFHT_Q	SHRB_Q	MAT-FEM_Q	LOGS_Q	RSPR_Q	DEND_Q	RSP-RAIN
E4	5	79.7	–	–	0	0.6172*	–	–	–	–	–	–	–	–	–
E2	6	80.3	–	–	1.52	0.2883*	–	–	–	–	–	–	–	–	–
C2	7	80.3	0	0.7187*	4.41	0.0680*	–	–	–	–	–	–	–	–	–
Global	9	82.3	1.88	0.2813*	6.29	0.0266	–	–	–	–	–	–	–	–	–
E6	4	61.7	–	–	24.14	<0.0001	–	–	–	–	–	–	–	–	–
E1	5	62.3	–	–	26.10	<0.0001	–	–	–	–	–	–	–	–	–
C6	6	64.2	22.22	<0.0001	26.64	<0.0001	–	–	–	–	–	–	–	–	–
C3	6	63.1	23.49	<0.0001	27.91	<0.0001	–	4.502	–	–	–	–	–	–	–
E5	4	57.1	–	–	28.97	<0.0001	–	–	–	–	–	–	–	–	24.878
C5	7	64.2	25.12	<0.0001	29.53	<0.0001	–	–	–	–	–	–	–	–	–
E3	5	58.8	–	–	29.83	<0.0001	9.128	–	–	–	–	–	–	–	–
E7	3	48.8	–	–	33.91	<0.0001	–	–	–	–	–	–	–	–	–
C1	7	58.3	31.51	<0.0001	35.92	<0.0001	7.659	–	–	–	–	–	–	–	–
C4	6	44.8	40.40	<0.0001	44.81	<0.0001	–	–	–	–	–	–	–	0.268	–
C7	5	34.7	44.77	<0.0001	49.18	<0.0001	13.507	–	1.189	−0.000	1.208	–	–	–	–
C8	6	28.9	51.06	<0.0001	55.47	<0.0001	–	–	–	−0.000	–	–	–	–	–
C10	5	22.2	52.10	<0.0001	56.51	<0.0001	–	–	–	–	–	0.0009	10.696	–	–
C9	5	17.9	54.38	<0.0001	58.79	<0.0001	–	–	1.156	−0.000	–	0.0011	–	–	–

[a] Linear regression models of long-tailed vole abundance described in Table 2.6.

[b] Number of model parameters estimated from data including intercept coefficient, effect coefficients, and a residual error term.

[c] Weighted according to minimum AIC_c value of the 11 *a priori* models.

[d] Weighted according to minimum AIC_c value of the 11 *a priori* and seven exploratory models.

Table 2.20 Precision and relative importance of ecological factors associated with summer abundance (g/ha) of long-tailed voles in the Sacramento Mountains, New Mexico (1992–1994). Two sets of regression coefficients ($\bar{\beta}$) are given; those averaged over *a priori* (original) models and the other averaged over original and exploratory (all) models. CVs of the average coefficients include variation associated with uncertainty of model structure. Relative importance (RI) of each regressor variable is also shown for both model sets and is based on the sums of Akaike weights for each model that included the regressor. Asterisks indicate effects included in the 95% confidence set of models. Regressor acronyms are defined in the text. Factors are ordered from highest to lowest according to RI in the original model set.

	Original Models			All Models		
Factor	$\bar{\beta}$	CV(%)	RI	$\bar{\beta}$	CV(%)	RI
MATFEM	35.200	14.9	1.000*	34.767	13.6	1.000*
INFCOMP	8.823	17.6	1.000*	8.901	17.2	1.000*
GFHT	−26.152	32.6	1.000*	−26.343	30.8	1.000*
FWTEMP	−41.208	91.3	1.000*	−13.918	112.7	0.383*
SHRUBS	0.0012	748.0	1.000*	0.0001	750.6	0.095*
LOGS	−0.113	93.4	0.281*	−0.011	114.1	0.027
ALTPREY	−0.0086	119.9	0.281*	−0.0008	136.7	0.027
MATFEM_Q	≈0.[a]	103.5	0.000	≈0.[a]	103.5	0.000
GFHT_Q	≈0.[a]	104.3	0.000	≈0.[a]	104.3	0.000
RSPR_Q	≈0.[a]	104.9	0.000	≈0.[a]	104.9	0.000
PSSRAIN	≈0.[a]	110.9	0.000	0.000002	106.5	0.000
DEND_Q	≈0.[a]	112.5	0.000	≈0.[a]	112.5	0.000
DENDEP	0.00003	131.2	0.000	0.000002	131.2	0.000
LOGS_Q	≈0.[a]	184.7	0.000	≈0.[a]	184.7	0.000
SHRB_Q	≈0.[a]	307.4	0.000	≈0.[a]	307.4	0.000
RSPRAIN	–	–	–	0.000008	106.4	0.000

[a] ≤0.000001

Table 2.21. Coefficients of modeled effects on summer abundance (g/ha) of Mexican woodrats in the Sacramento Mountains, New Mexico (1992–1994) and weights of model reliability. Sample size (n = 42) is based on 20 sites each sampled during 1, 2 or 3 summers. Model order based on ΔAIC_c. Regressor variables are described in the text and Table 2.7.

MW[a]		R^2	Original Models[c]		All Models[d]		INTER-				MAT-	
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	CEPT	CSAPL	SHRUBS	GFHT	FEM	ROCKS
E7	3	67.3	–	–	0	0.3873*	20.271	–	–	–	61.295	–
E6	4	68.2	–	–	1.30	0.2021*	−5.460	–	–	–	61.288	–
E4	4	67.5	–	–	2.13	0.1333*	28.118	–	–	–	63.051	−0.329
E5	4	67.4	–	–	2.34	0.1204*	22.717	–	–	–	61.606	–
E3	5	68.2	–	–	3.81	0.0576*	−3.080	–	–	–	61.540	–
E1	5	67.8	–	–	4.34	0.0442*	36.734	–	–	–	64.508	−0.486
E2	6	68.5	–	–	6.18	0.0176*	10.510	–	–	–	63.850	−0.386
C5	6	68.1	0	0.3597*	6.71	0.0135	34.203	–	−0.0018	–	64.324	−0.238
C10	6	67.8	0.32	0.3065*	7.03	0.0115	34.315	–	–	–	64.430	−0.448
C1	7	68.2	2.76	0.0905*	9.47	0.0034	14.800	–	−0.0018	0.737	62.669	−0.009
C4	7	68.1	2.89	0.0846*	9.61	0.0032	34.379	–	−0.0018	–	64.317	−0.240
C3	7	68.0	3.07	0.0776*	9.78	0.0029	22.858	0.006	−0.0020	–	63.092	−0.125
C2	7	67.9	3.09	0.0766*	9.81	0.0029	11.642	–	–	0.932	62.617	−0.144
Global	9	68.4	8.81	0.0044	15.53	0.0002	18.862	0.016	−0.0016	0.799	62.621	−0.337
C7	6	18.3	39.49	<0.0001	46.20	<0.0001	−38.784	0.092	–	–	–	0.519
C6	6	18.2	39.52	<0.0001	46.24	<0.0001	−31.291	0.096	−0.0007	–	–	0.456
C11	7	20.2	41.38	<0.0001	48.10	<0.0001	−56.400	0.094	−0.0014	3.463	–	1.480
C8	7	17.7	42.68	<0.0001	49.40	<0.0001	−49.598	0.113	−0.0007	2.731	–	0.721
C9	8	23.3	42.80	<0.0001	49.51	<0.0001	226.828	0.084	−0.0003	–	–	−0.267

Table 2.21. (Continued).

MW[a] Model	K[b]	R^2 (%)	Original Models[c] ΔAIC_c	Original Models[c] Weight	All Models[d] ΔAIC_c	All Models[d] Weight	LGLOG	DEN-DEP	ALT-PREY	MTM-GOK	FW-TEMP	RSP-RAIN
E7	3	67.3	–	–	0	0.3873*	–	–	–	–	–	–
E6	4	68.2	–	–	1.30	0.2021*	–	–	–	–	–	2.301
E4	4	67.5	–	–	2.13	0.1333*	–	–	–	–	–	–
E5	4	67.4	–	–	2.34	0.1204*	−0.121	–	–	–	–	–
E3	5	68.2	–	–	3.81	0.0576*	−0.098	–	–	–	–	2.265
E1	5	67.8	–	–	4.34	0.0442*	−0.241	–	–	–	–	–
E2	6	68.5	–	–	6.18	0.0176*	−0.195	–	–	–	–	2.049
C5	6	68.1	0	0.3597*	6.71	0.0135	−0.189	–	–	–	–	–
C10	6	67.8	0.32	0.3065*	7.03	0.0115	−0.252	–	–	0.0037	–	–
C1	7	68.2	2.76	0.0905*	9.47	0.0034	–	3.854	–	–	–	–
C4	7	68.1	2.89	0.0846*	9.61	0.0032	−0.190	–	−0.0001	–	–	–
C3	7	68.0	3.07	0.0776*	9.78	0.0029	–	–	0.0016	–	–	–
C2	7	67.9	3.09	0.0766*	9.81	0.0029	–	3.129	–	0.0017	–	–
Global	9	68.4	8.81	0.0044	15.53	0.0002	−0.172	3.621	–	–	–	–
C7	6	18.3	39.49	<0.0001	46.20	<0.0001	–	–	–	0.0072	–	4.812
C6	6	18.2	39.52	<0.0001	46.24	<0.0001	–	–	–	–	–	4.603
C11	7	20.2	41.38	<0.0001	48.10	<0.0001	0.796	–	–	–	–	–
C8	7	17.7	42.68	<0.0001	49.40	<0.0001	–	–	–	–	−4.377	–
C9	8	23.3	42.80	<0.0001	49.51	<0.0001	0.877	–	–	–	48.250	9.519

[a] Linear regression models of Mexican woodrat abundance described in Table 2.7.

[b] Number of model parameters estimated from data including intercept coefficient, effect coefficients, and a residual error term.

[c] Weighted according to minimum AIC_c value of the 12 *a priori* models.

[d] Weighted according to minimum AIC_c value of the 12 *a priori* and seven exploratory models.

Table 2.22 Precision and relative importance of ecological factors associated with summer abundance (g/ha) of Mexican woodrats in the Sacramento Mountains, New Mexico (1992–1994). Two sets of regression coefficients ($\bar{\beta}$) are given; those averaged over *a priori* (original) models and the other averaged over original and exploratory (all) models. CVs of the average coefficients include variation associated with uncertainty of model structure. Relative importance (RI) of each regressor variable is also shown for both model sets and is based on the sums of Akaike weights for each model that included the regressor. Asterisks indicate effects included in the 95% confidence set of models. Regressor acronyms are defined in the text. Factors are ordered from highest to lowest according to RI in the original model set.

	Original Models			All Models		
Factor	$\bar{\beta}$	CV(%)	RI	$\bar{\beta}$	CV(%)	RI
MATFEM	63.972	12.7	1.000*	61.867	11.4	1.000*
ROCKS	−0.264	297.0	1.000*	−0.082	201.1	0.233*
LGLOG	−0.162	200.5	0.755*	−0.040	269.9	0.268*
SHRUBS	−0.00110	180.8	0.617*	−0.0000 4	201.9	0.023
MTMGOK	0.00125	604.3	0.383*	0.00005	609.2	0.014
GFHT	0.142	192.2	0.172*	0.005	199.8	0.006
DENDEP	0.604	356.9	0.172*	0.023	361.1	0.006
ALTPREY	0.000119	1,135.2	0.162*	0.000004	1,136.4	0.006
CSAPL	0.00056	571.3	0.082*	0.00002	572.6	0.003
FWTEMP	≈0.[a]	199.7	0.000	≈0.[a]	199.7	0.000
RSPRAIN	≈0.[a]	126.6	0.000	0.632	121.5	0.277*

[a] ≤0.000001

Table 2.23. Regressor variables ranked as most important effects on summer abundance (g/ha) of five rodent species in the Sacramento Mountains, New Mexico, during 1992–1994. Two sets of effects are shown, those determined from *a priori* (original) models and those from original and exploratory (all) models.

	Original Models				All Models			
Species	Effect[a]	RI[b]	CV%[c]	Sign[d]	Effect[a]	RI[b]	CV%[c]	Sign[d]
Deer mouse	MCONIF	1.000	164.1	−, ?	MATFEM	0.997	23.7	+, +*
	PREVRAIN	1.000	329.7	−, +*	FWTEMP	0.954	48.7	−, −
	MATFEM	0.998	23.3	+, +*	GFHT	0.848	113.2	+, +*
Brush mouse	MATFEM	1.000	6.8	+, +*	MATFEM	1.000	7.3	+, +*
	ROCKS	1.000	354.6	+, +*	ROCKS	0.710	299.6	−, +*
	SHRUBS	0.868	11,095.0	+, +*	OAKS	0.436	681.8	+, +*
Mexican vole	GFHT	1.000	17.7	+, +*	GFHT	1.000	17.8	+, +*
	MATFEM	1.000	18.3	+, +*	MATFEM	1.000	18.5	+, +*
	INFCOMP	1.000	20.5	+, +*	INFCOMP	1.000	20.5	+, +*
Long-tailed vole	MATFEM	1.000	14.9	+, +*	MATFEM	1.000	13.6	+, +*
	INFCOMP	1.000	17.6	+, +*	INFCOMP	1.000	17.2	+, +*
	GFHT	1.000	32.6	−, +*	GFHT	1.000	30.8	−, +*
	FWTEMP	1.000	91.3	−, ∧				
	SHRUBS	1.000	748.0	+, −				
Mexican woodrat	MATFEM	1.000	12.7	+, +*	MATFEM	1.000	11.4	+, +*
	ROCKS	1.000	297.0	−, ∧				
	LGLOG	0.755	200.5	−, ?				
	SHRUBS	0.617	180.8	−, ?				

[a] MCONIF—density ($\hat{N}$/ha) of mature conifers; PREVRAIN—total rainfall (cm) during two previous growing seasons (March–August); MATFEM—number of reproductively active females in the summer population; FWTEMP—mean minimum temperature (°C) during late fall and winter; GFHT—mean maximum height (cm) of grasses or forbs; ROCKS—mean percentage of rock cover (arcsine-square root transformed); SHRUBS—density of all shrubs; OAKS—density of shrub and tree-sized oaks; INFCOMP—density of species likely to interfere with use of space during the same summer; LGLOG— density of logs >30 cm in diameter at mid-point.

[b] Relative importance based on Akaike weights of models for a given species.

[c] Coefficient of variation of model-averaged estimates of effect coefficients.

[d] Sign of model-averaged coefficient followed by sign of relationship in bivariate plots of indicated variable with summer abundance of listed species; ∧ indicates a quadratic relationship and ? indicates an unclear relationship; * denotes agreement of bivariate relationships with envirogram predictions.

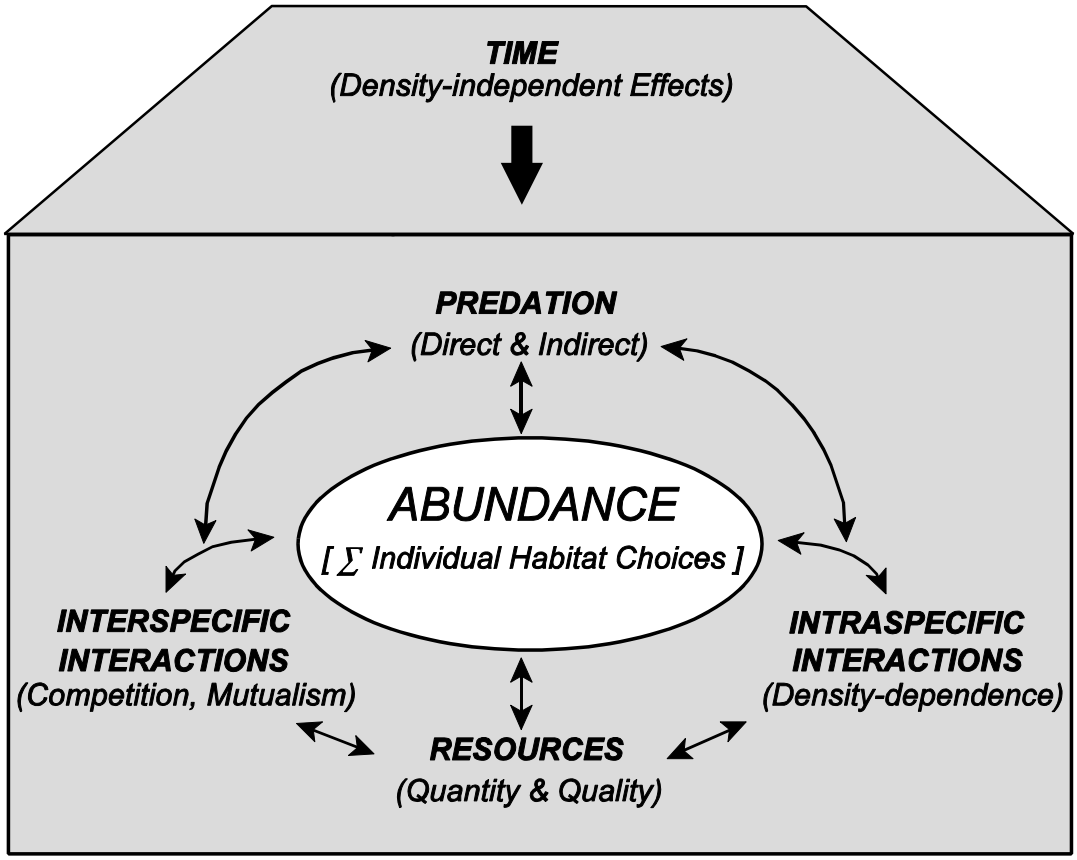

Figure 2.1. Ecological processes that affect the abundance of small mammals.

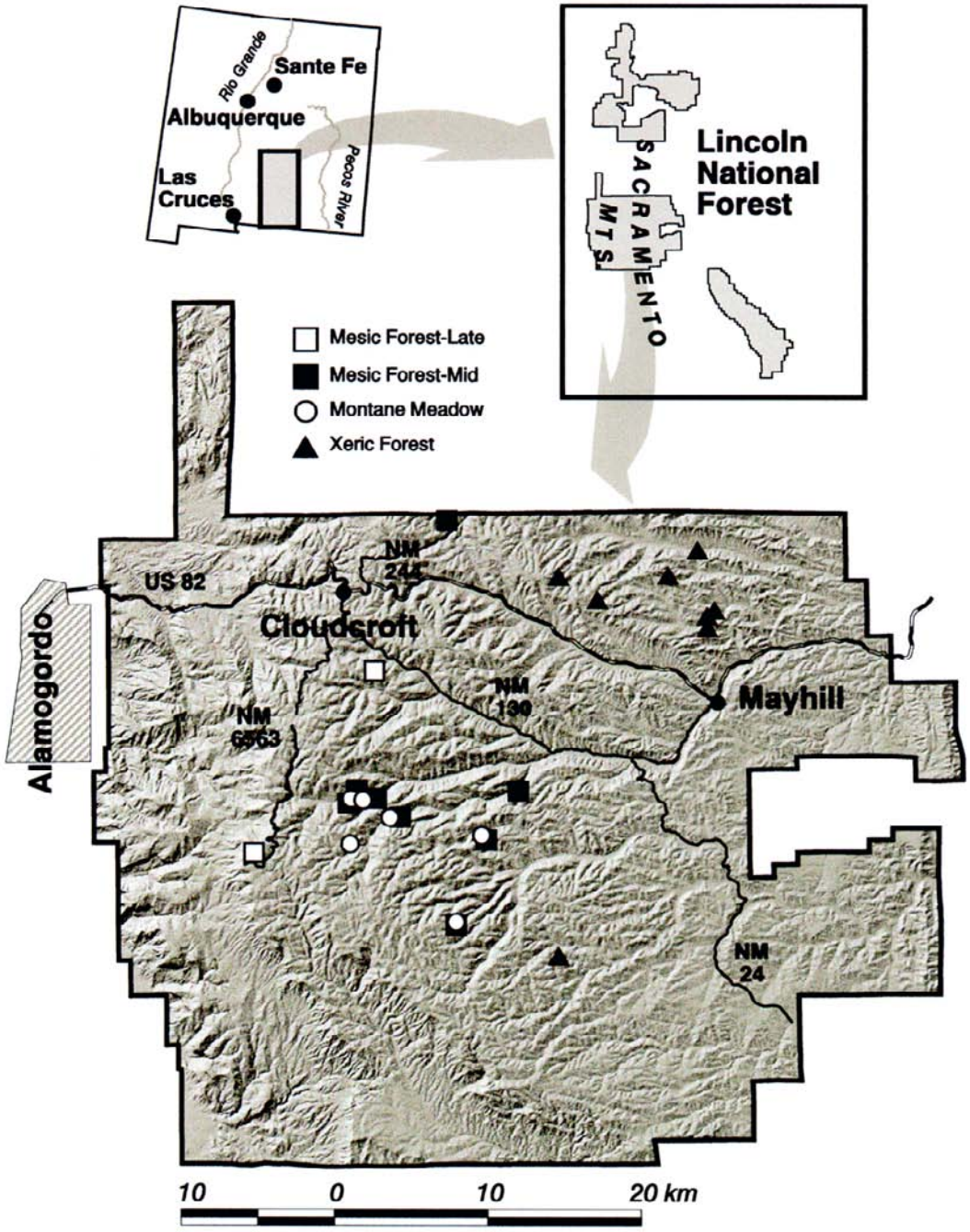

Figure 2.2. General vicinity of the study area and specific location of small mammal trapping girds in the Sacramento Mountains, New Mexico.

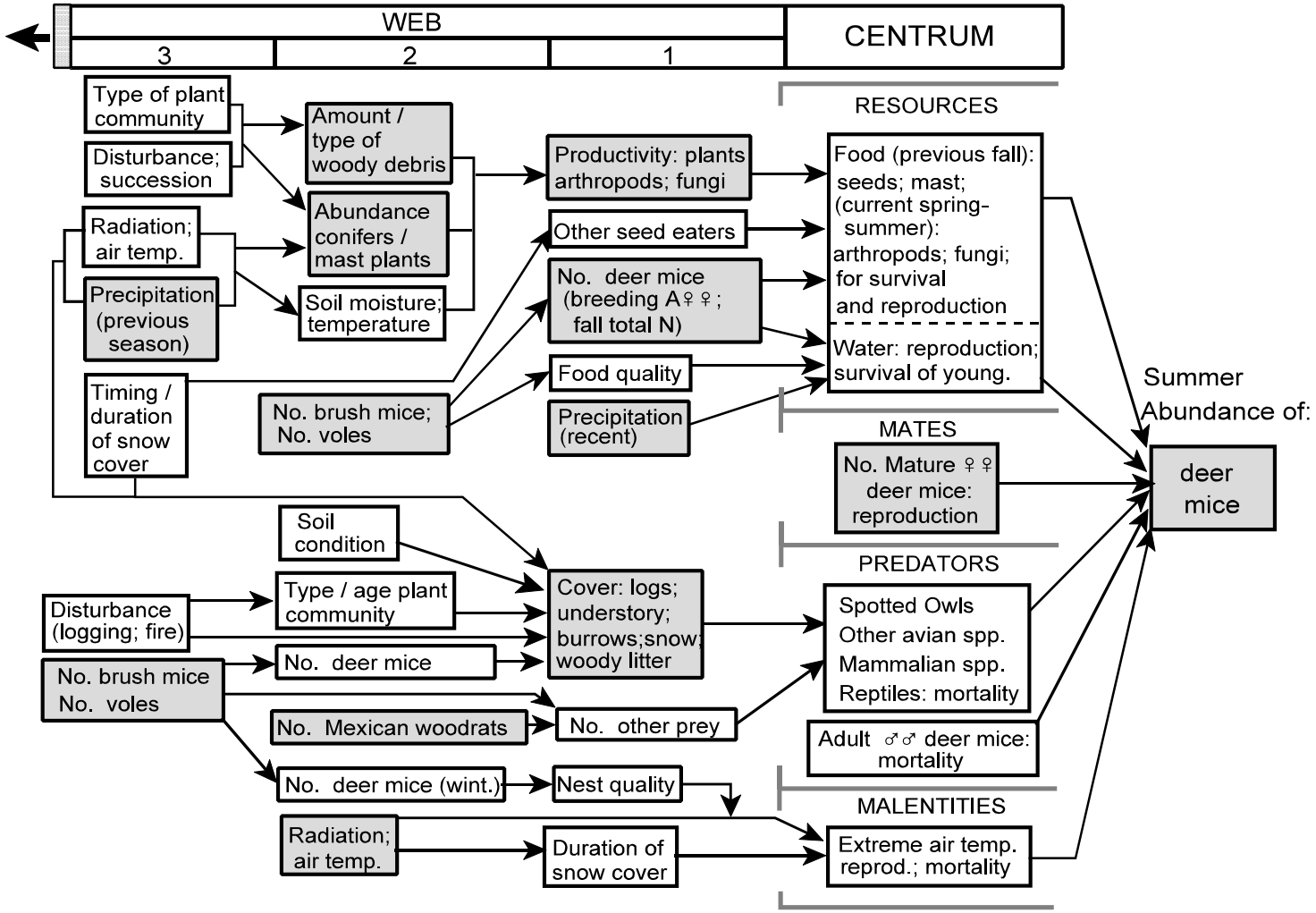

Figure 2.3. Envirogram depicting direct and indirect effects on deer mouse abundance developed from existing literature. Shaded boxes indicate information that was included in models.

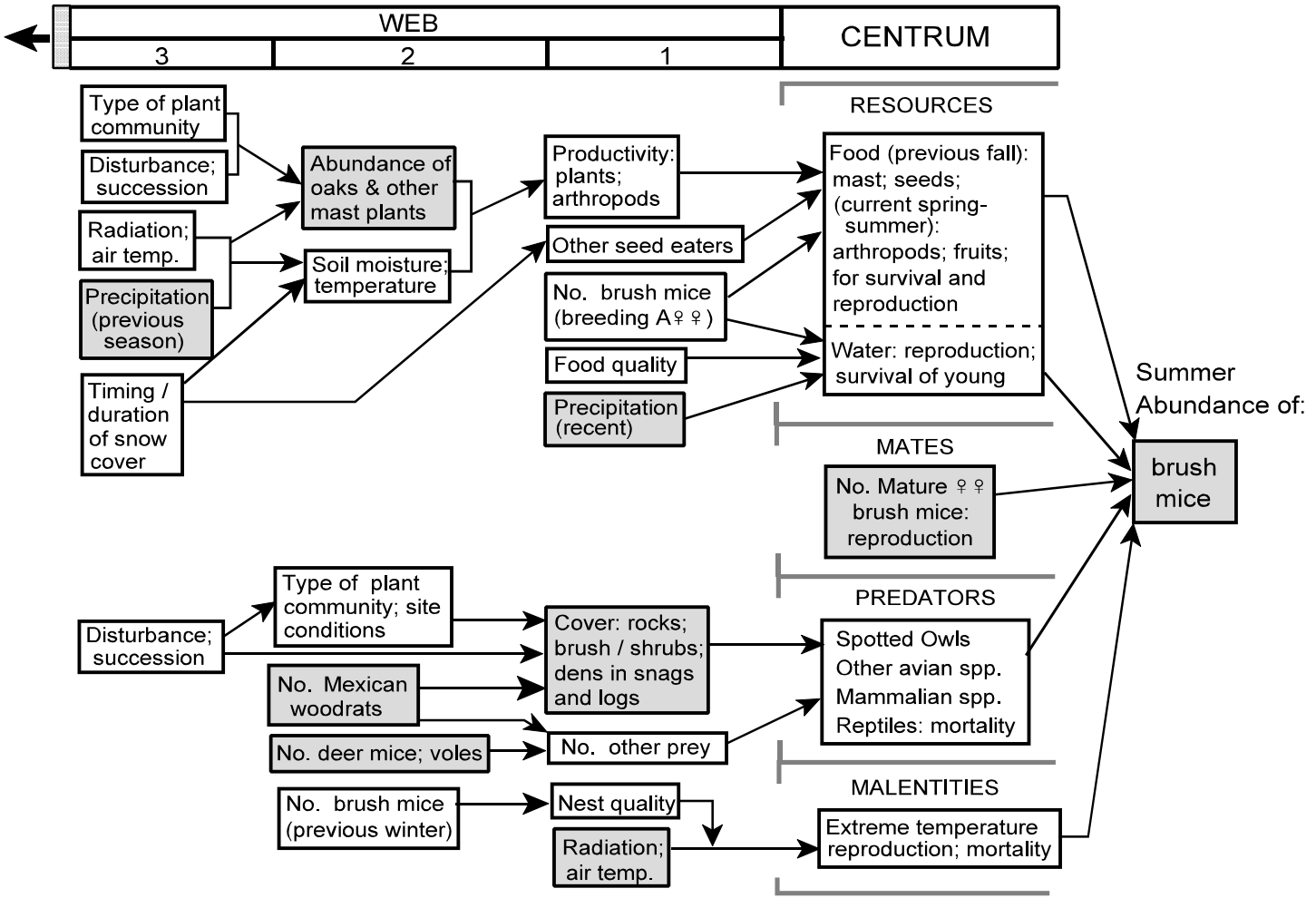

Figure 2.4. Envirogram depicting direct and indirect effects on brush mouse abundance developed from existing literature. Shaded boxes indicate information that was included in models.

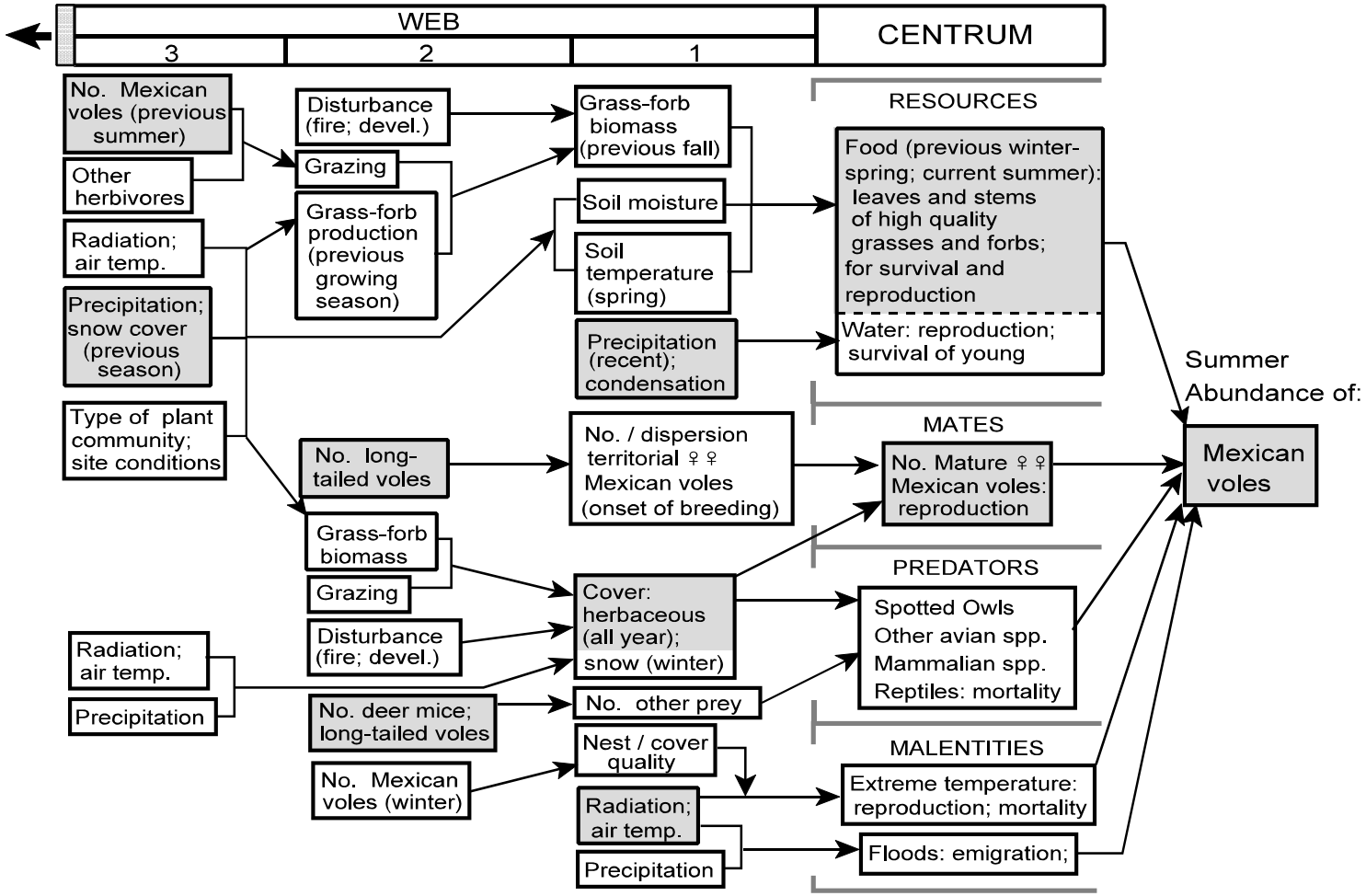

Figure 2.5. Envirogram depicting direct and indirect effects on Mexican vole abundance developed from existing literature. Shaded boxes indicate information that was included in models.

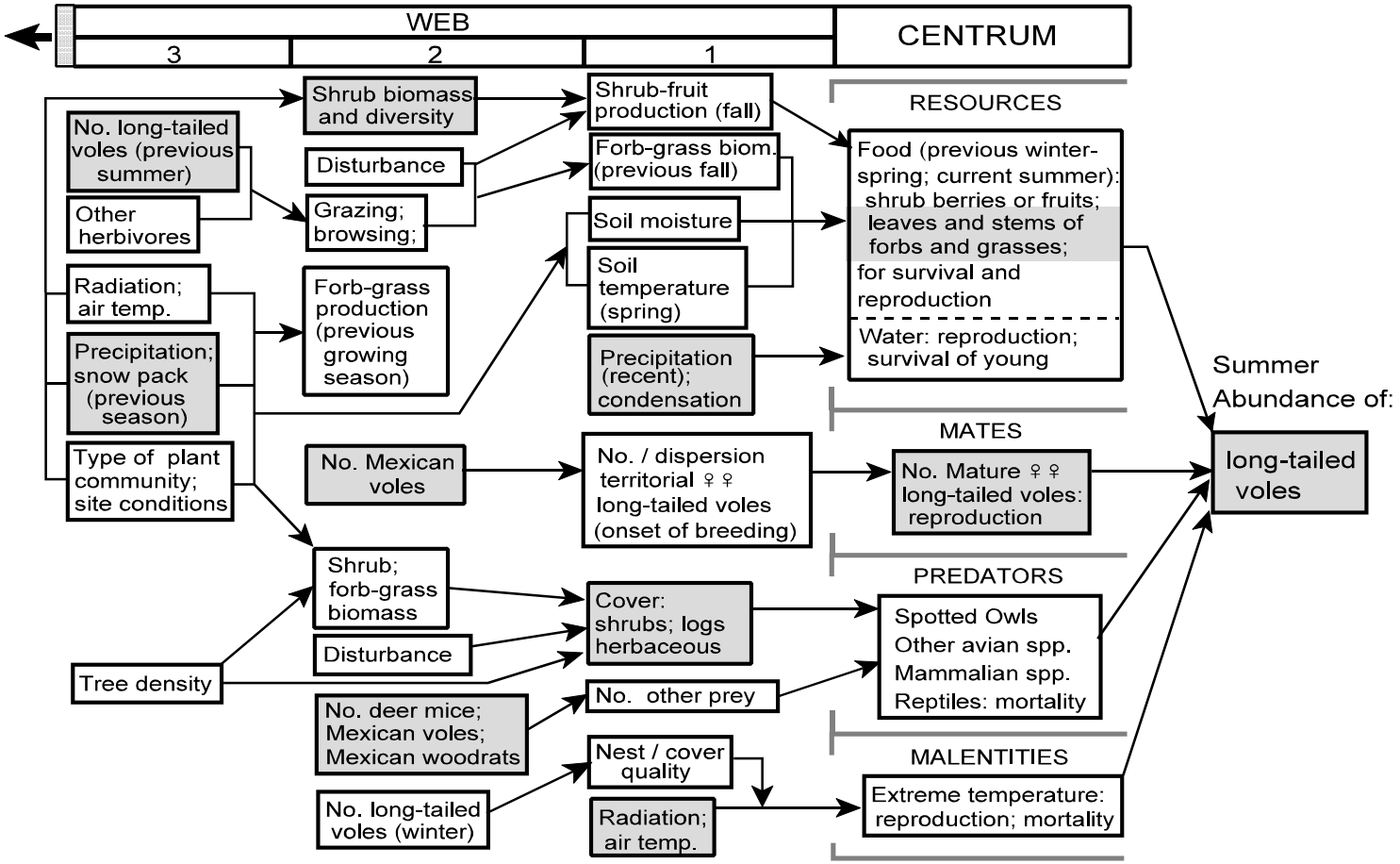

Figure 2.6. Envirogram depicting direct and indirect effects on long-tailed vole abundance developed from existing literature. Shaded boxes indicate information that was included in models.

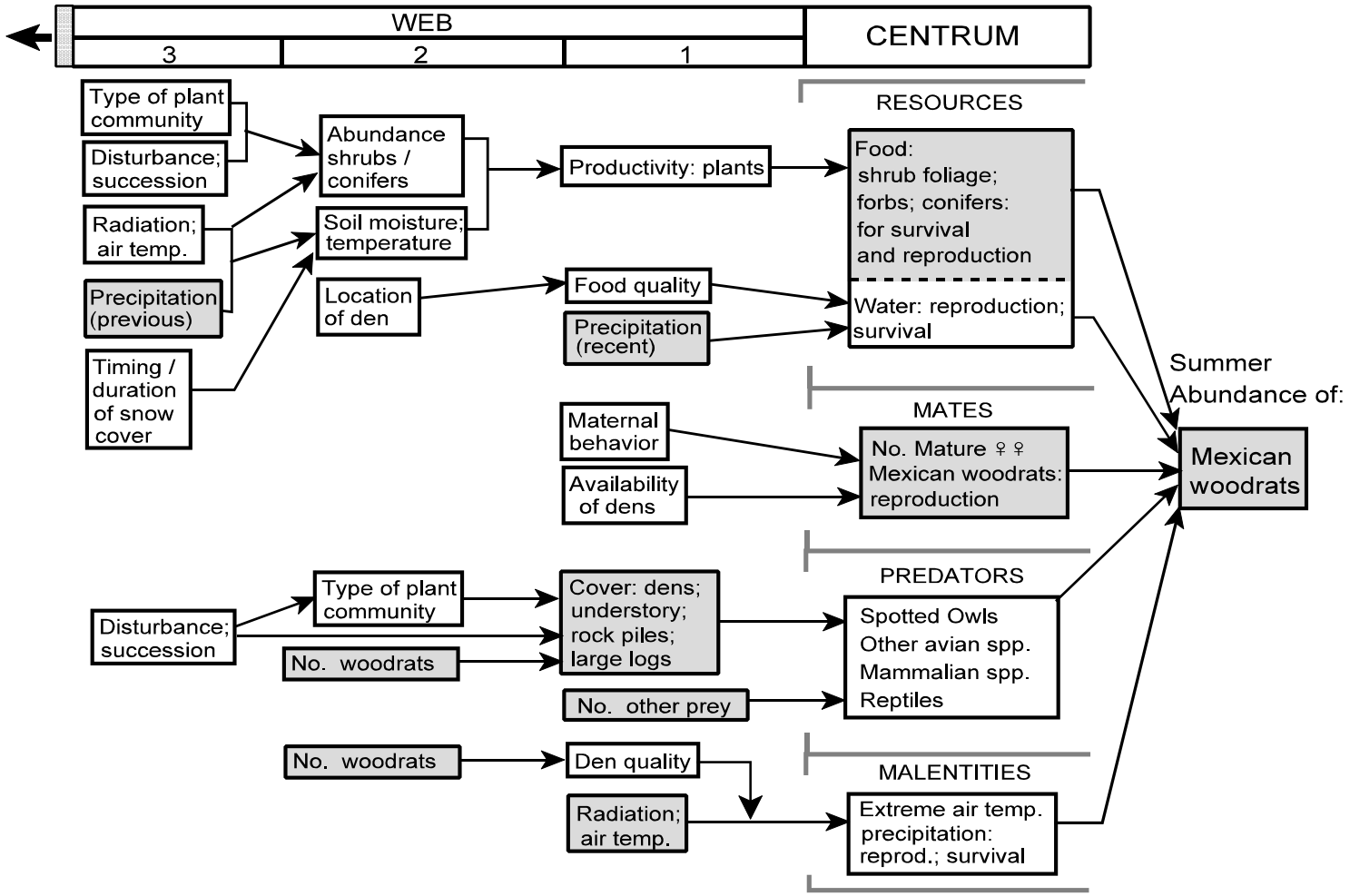

Figure 2.7. Envirogram depicting direct and indirect effects on Mexican woodrat abundance developed from existing literature. Shaded boxes indicate information that was included in models.

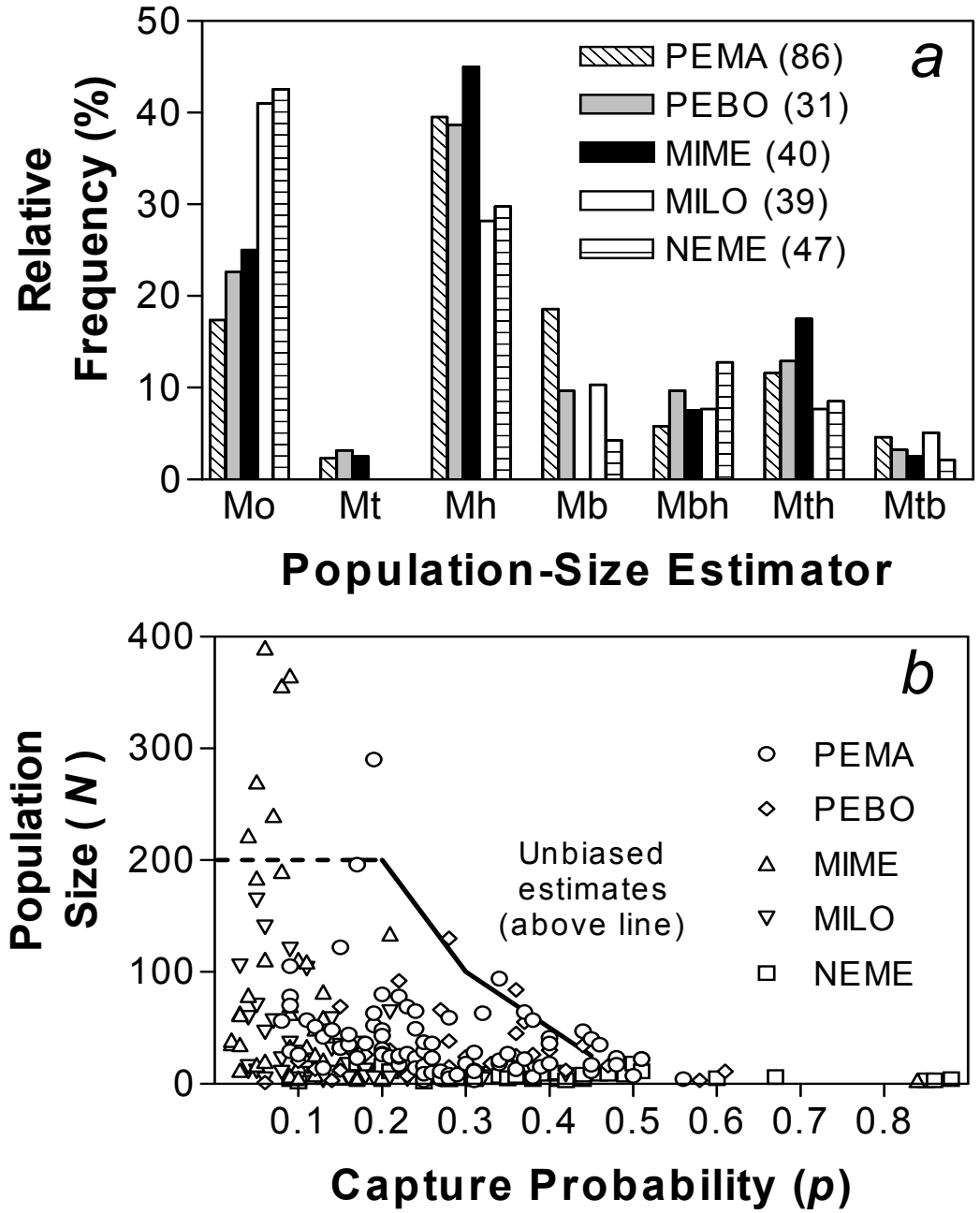

Figure 2.8. Frequency of models (*a*) selected for estimating population sizes of five murid rodents in the Sacramento Mountains, New Mexico (1991–1996) and reliability of estimates of sampling error in abundance estimates (*b*) from 243 analyzed data sets. The various models (M_) assume equal and constant capture probability ($\hat{p}$) among individuals (o), or variation in $\hat{p}$ caused by time (t), by behavioral response to initial capture (b), or by biological differences (e.g., sex, age) among individuals (h). Species acronyms are PEMA–deer mouse, PEBO–brush mouse, MIME–Mexican vole, MILO–long-tailed vole, and NEME– Mexican woodrat. Number of data sets for each species are shown in parentheses (*a*).

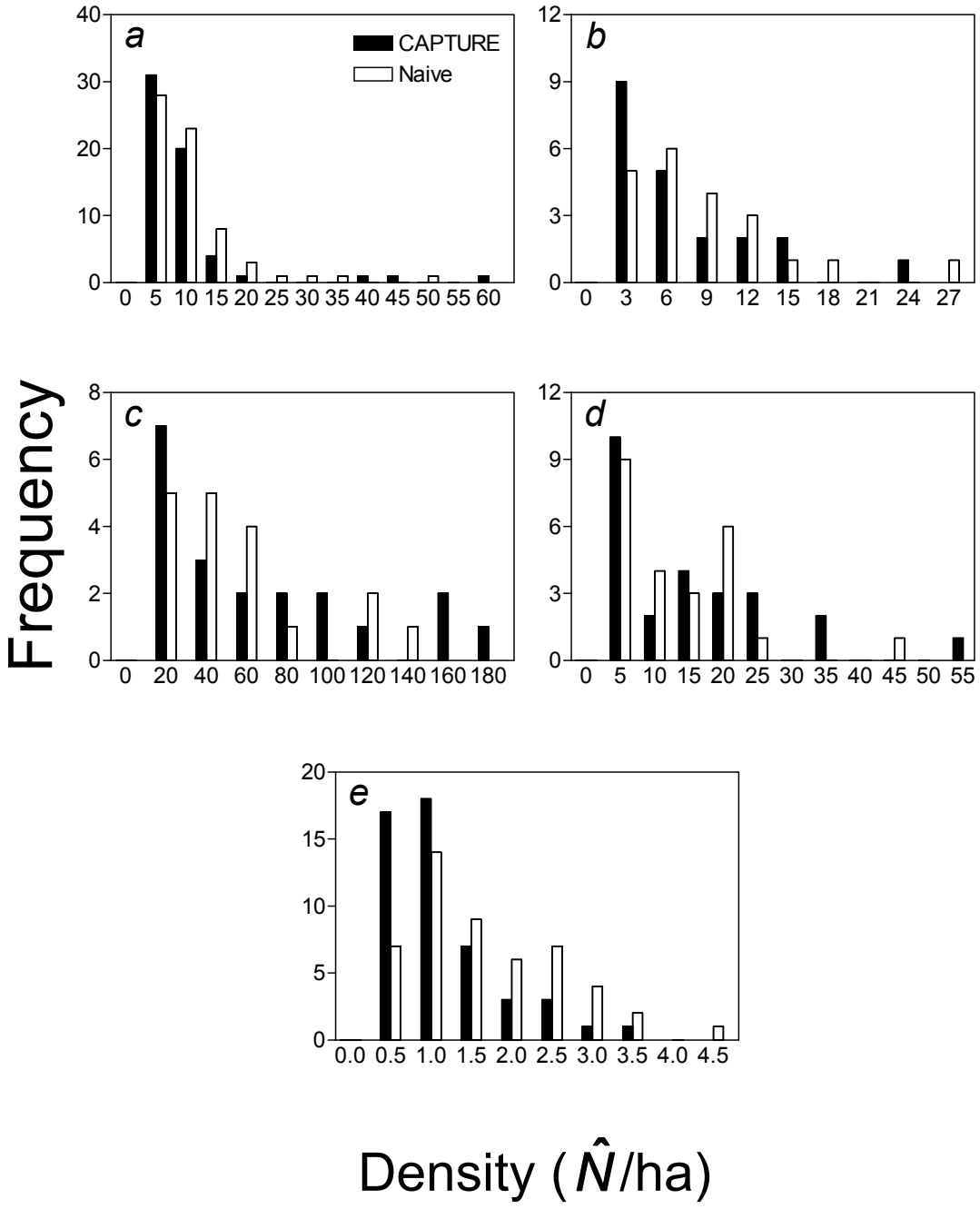

Figure 2. 9. Distribution of summer densities of five small species (*a*) deer mice; (*b*) brush mice; (*c*) Mexican voles; (*d*) long-tailed voles; and (*d*) Mexican woodrats estimated using closed-population sizes divided by effective sampling area (using Program CAPTURE) or number of individuals marked divided by grid area (Naive) from the Sacramento Mountains, New Mexico (1991–1996). Zero estimates for sites where the species was not observed have been excluded.

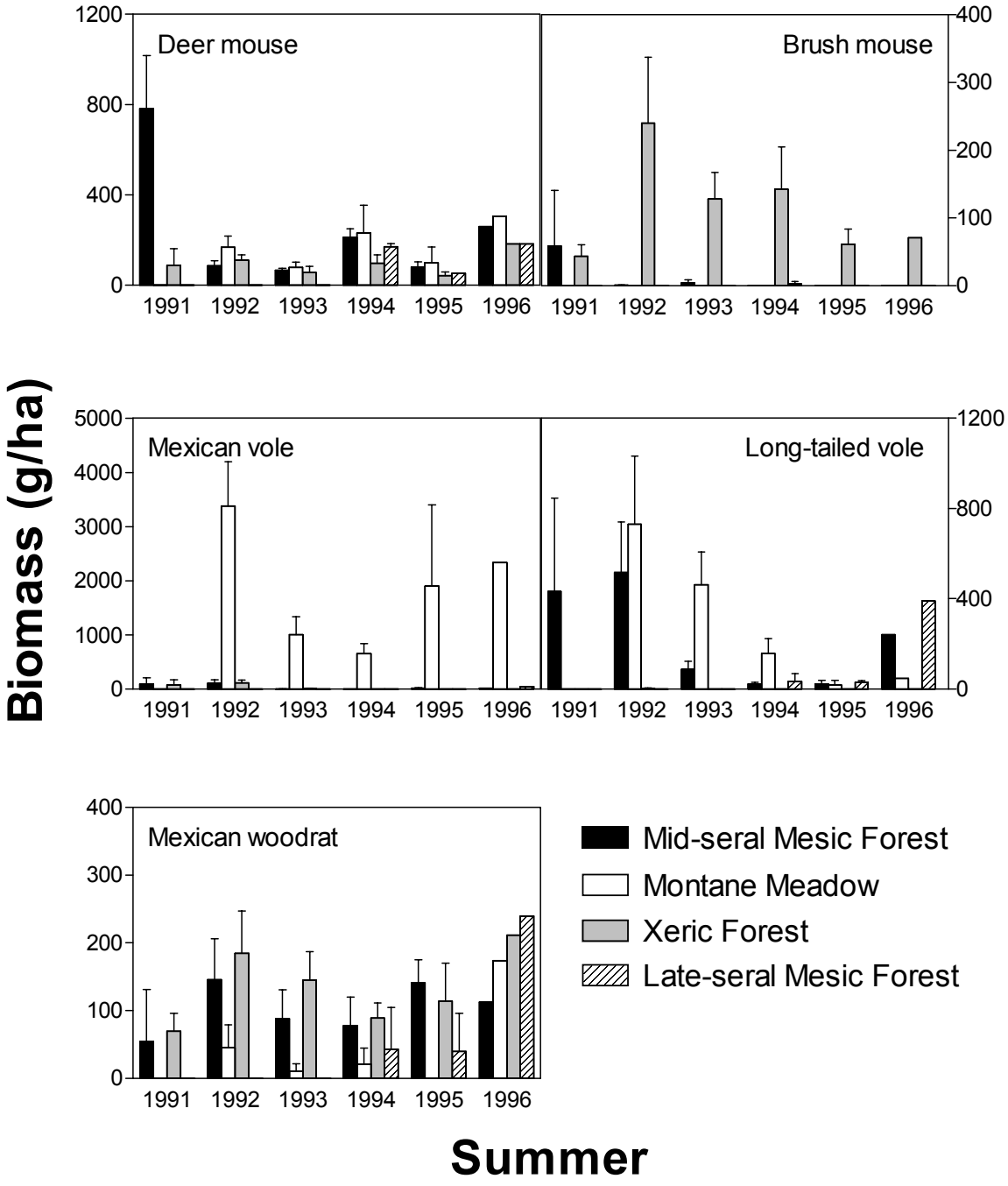

Figure 2.10. Annual patterns in the distribution and abundance of five murid rodents occurring in the Sacramento Mountains, New Mexico during July–August (1991–1996). Error bars are SE of mean biomass among replicate sites within each habitat. Number of replicates is given in Table 2.1. Ordinate scale varies by species. Montane meadows were not sampled in 1991.

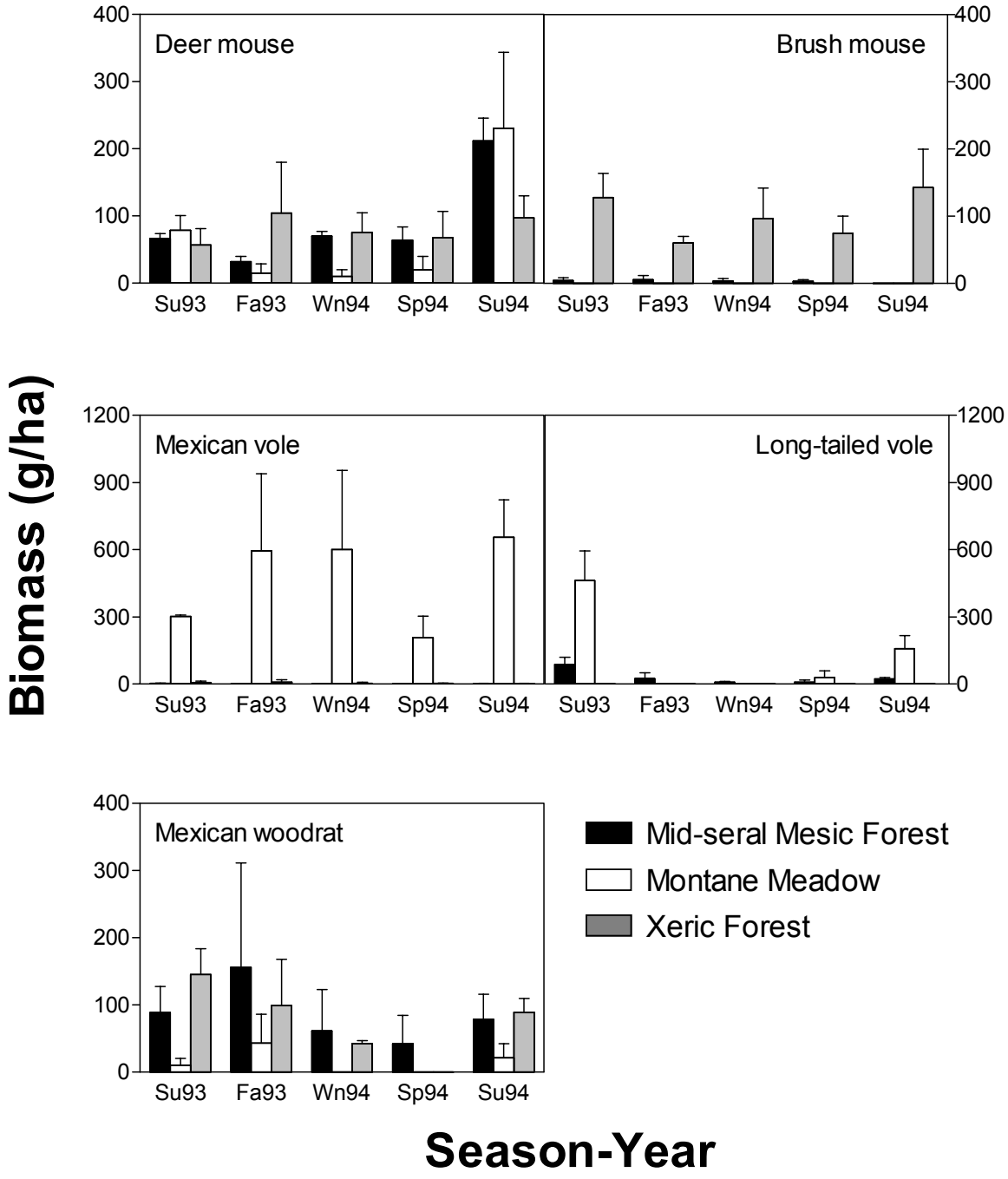

Figure 2.11. Seasonal patterns in the distribution and abundance of five murid rodents occurring in the Sacramento Mountains, New Mexico during one annual period (1993–1994). Summer (Su) was sampled during mid-July through mid-Aug; fall (Fa) during mid-October through mid-November; winter (Wn) during mid-January through mid-February; spring (Sp) during mid-April through mid-May. Error bars are SE of mean biomass among replicate sites within each habitat. Number of replicates is given in Table 2.1. Ordinate scale varies by species.

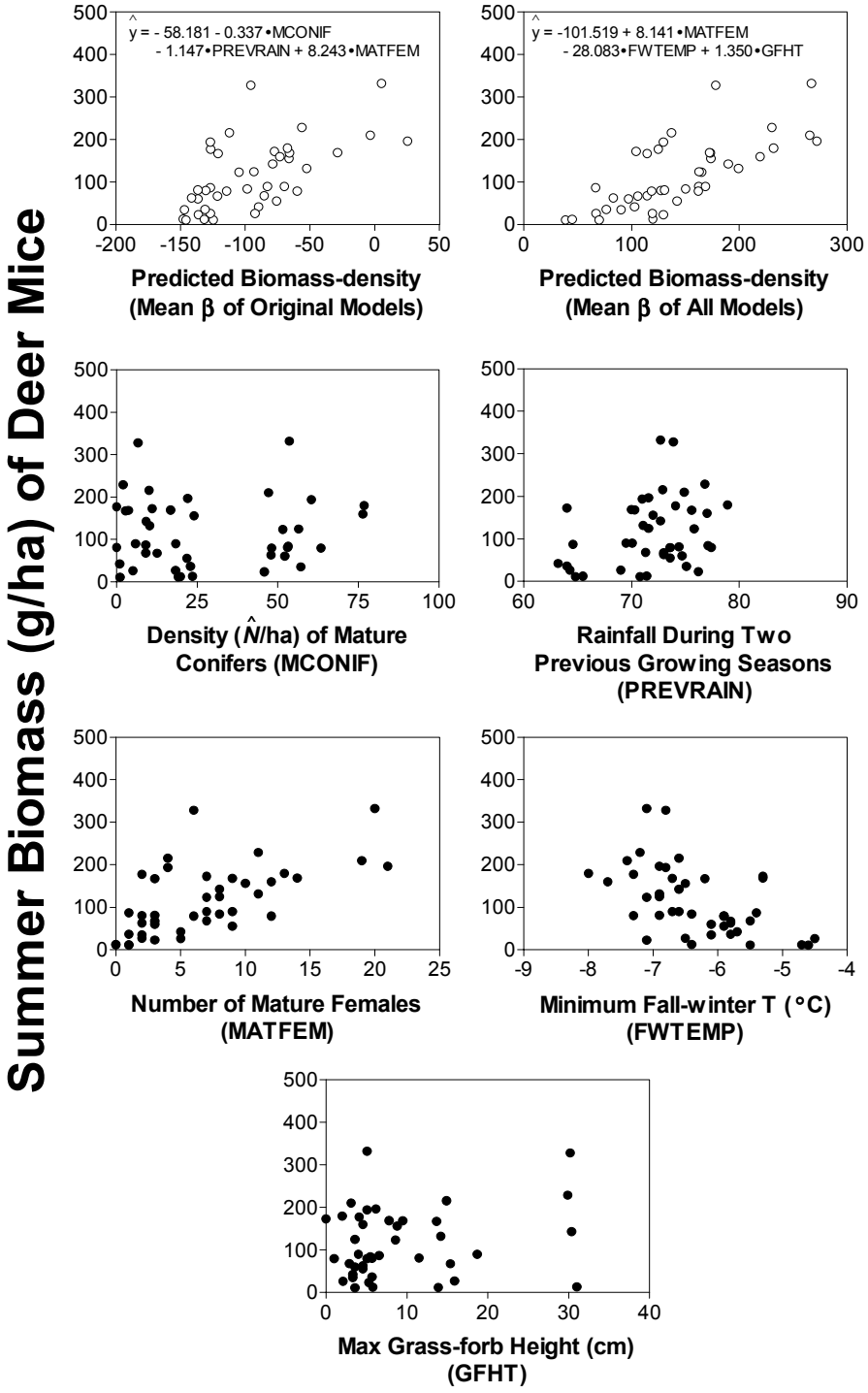

Figure 2.12. Fit of *a priori* (original) and all (original and exploratory) models predicting summer abundance of deer mice from likely biotic and abiotic factors in the Sacramento Mountains, New Mexico (1992–1994). Effect coefficients ($\bar{\beta}$) are averages across models in the indicated set. Bivariate plots between deer mouse abundance and each of the highest ranked independent regressor variables are also shown (n = 42 combinations of site and year).

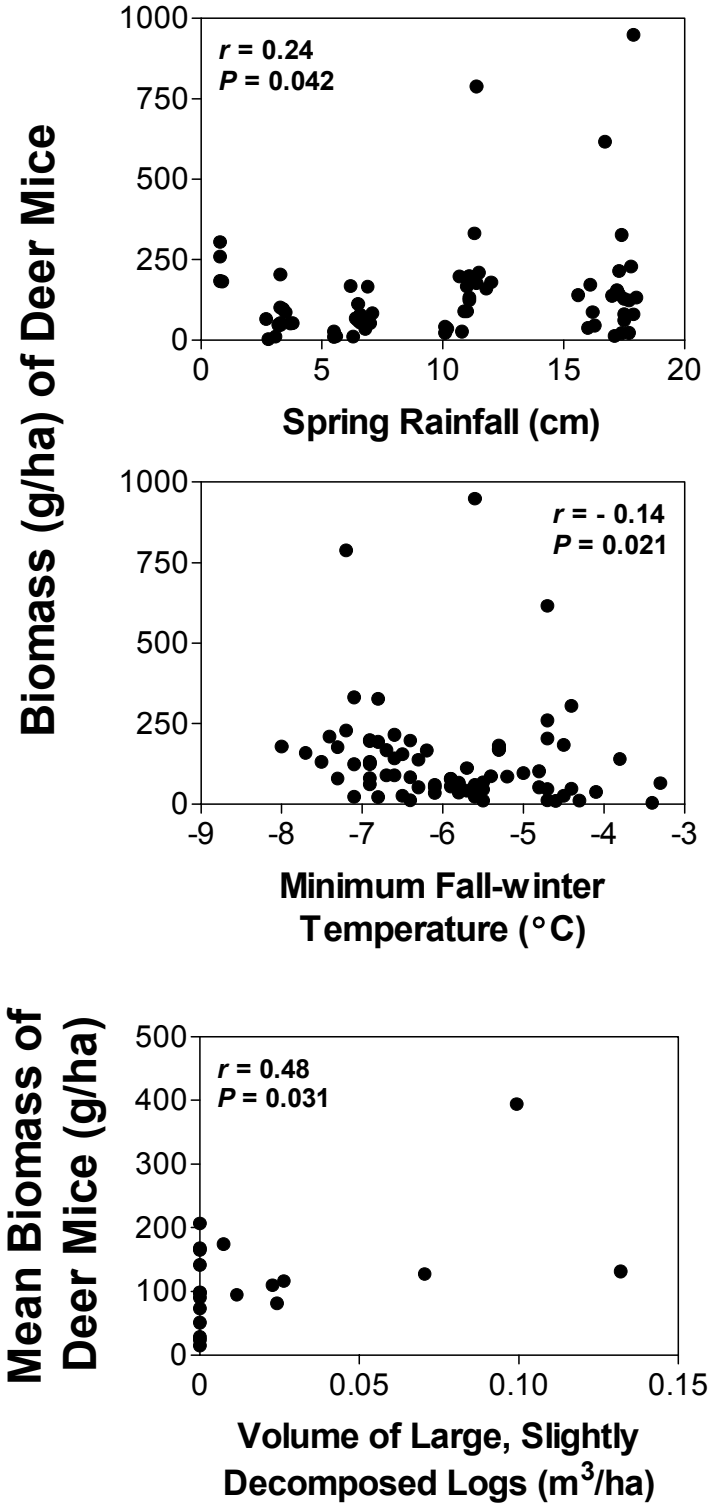

Figure 2.13. Additional correlations between deer mouse abundance and selected weather or microhabitat variables in the Sacramento Mountains, New Mexico (1991–1996).

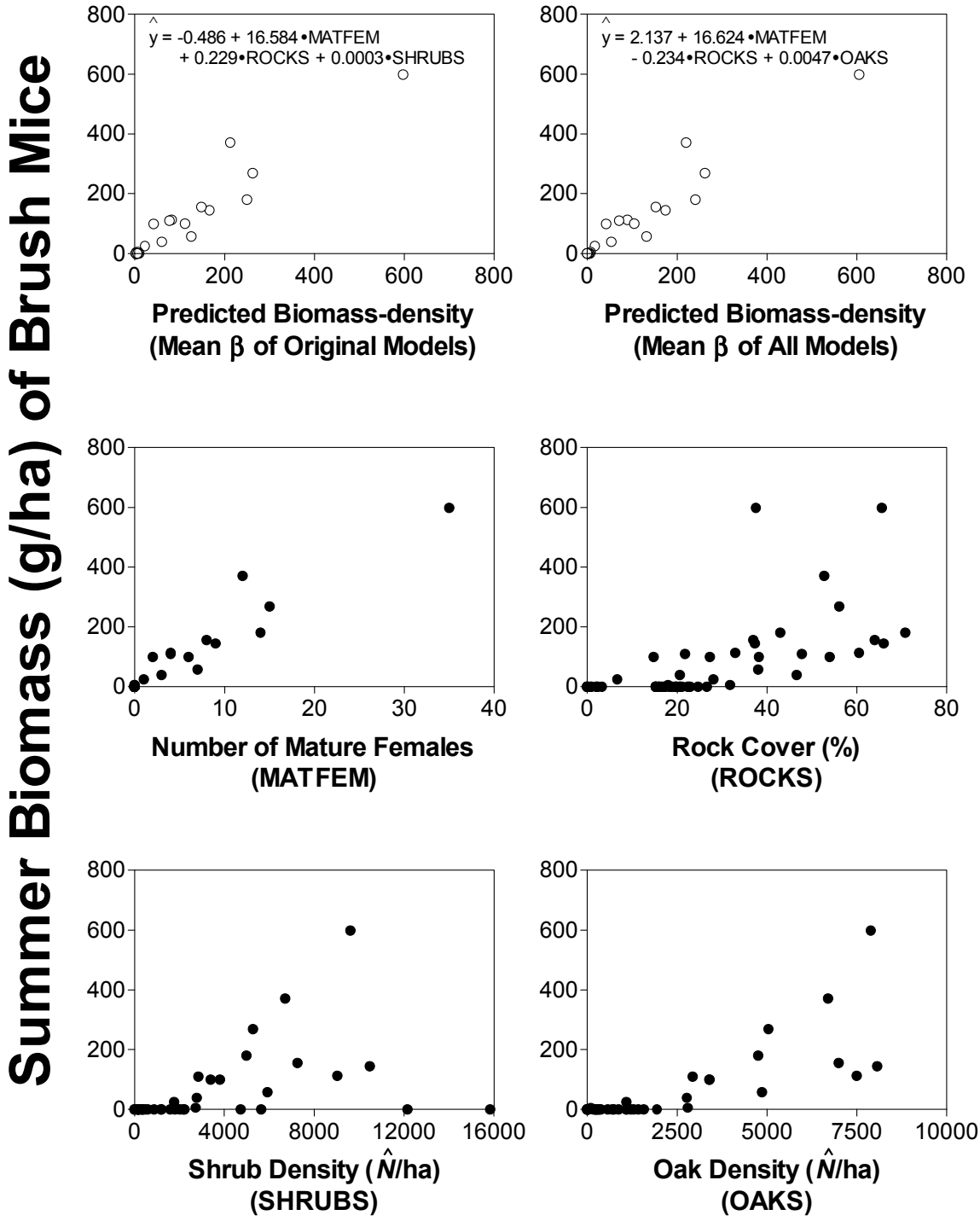

Figure 2.14. Fit of *a priori* (original) and all (original and exploratory) models predicting summer abundance of brush mice from likely biotic and abiotic factors in the Sacramento Mountains, New Mexico (1992–1994). Effect coefficients ($\bar{\beta}$) are averages across models in the indicated set. Bivariate plots between brush mouse abundance and each of the highest ranked independent regressor variables are also shown (n = 42 combinations of site and year).

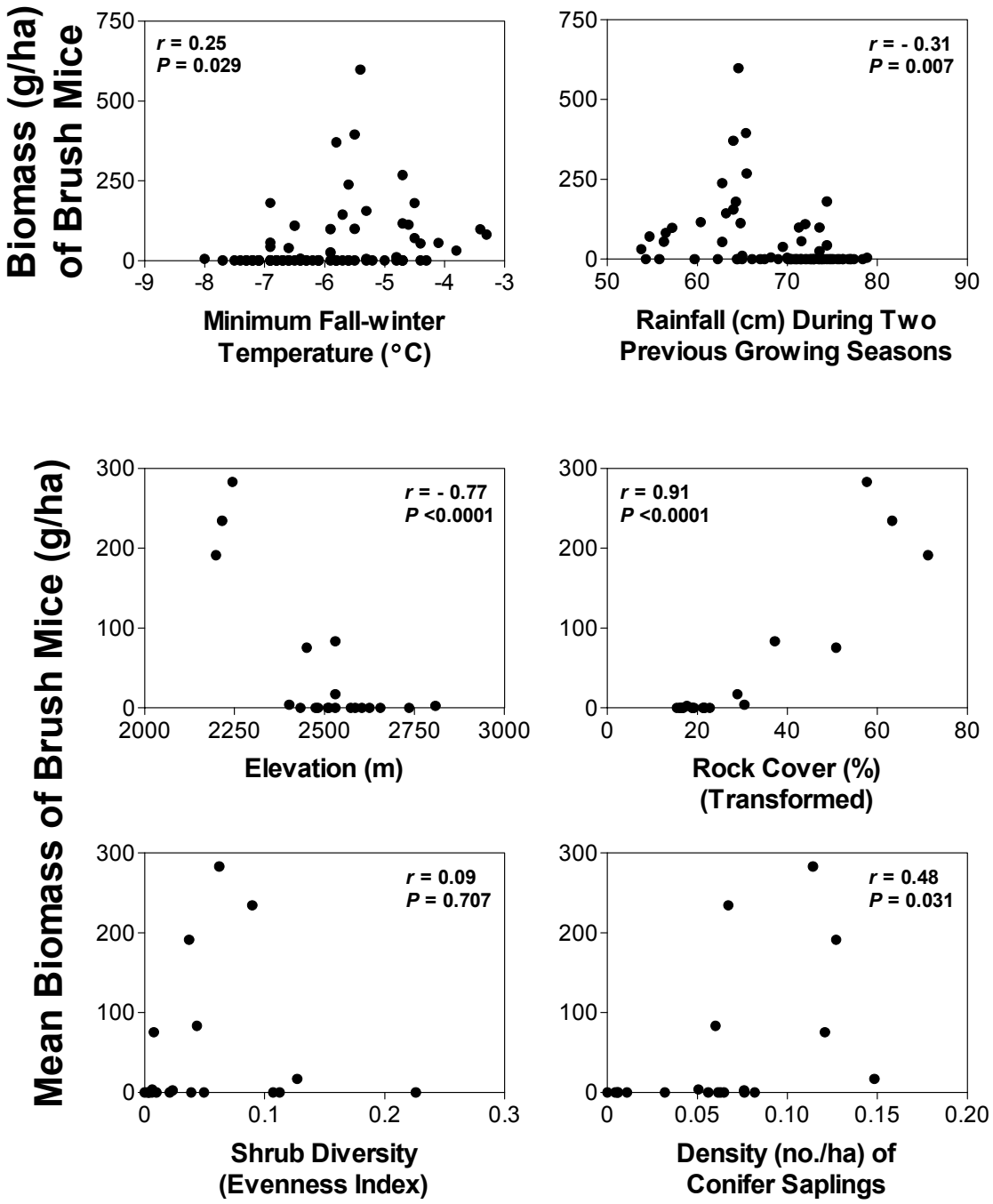

Figure 2.15. Additional correlations between brush mouse abundance and selected weather or microhabitat variables in the Sacramento Mountains, New Mexico (1991–1996).

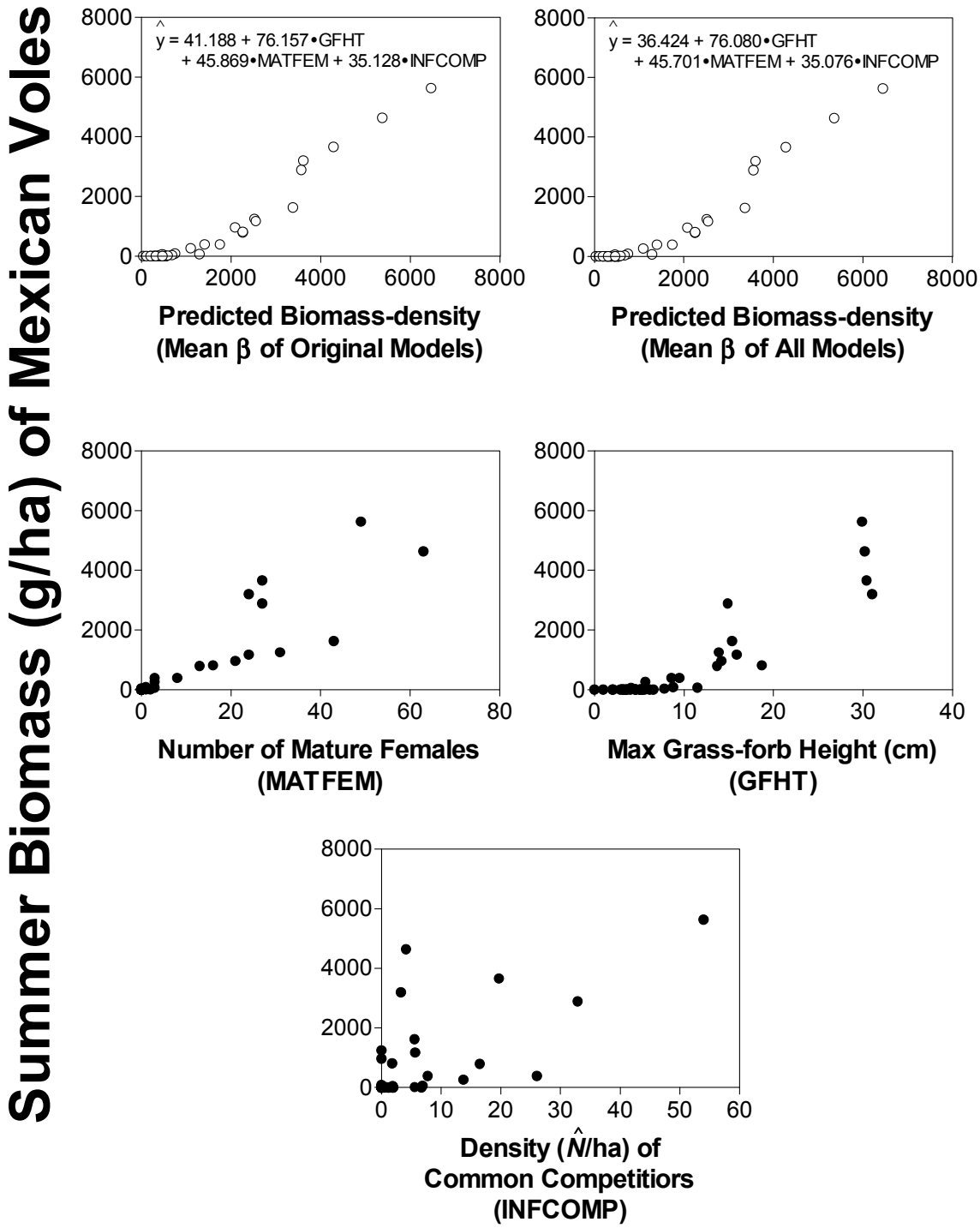

Figure 2.16. Fit of *a priori* (original) and all (original and exploratory) models predicting summer abundance of Mexican voles from likely biotic and abiotic factors in the Sacramento Mountains, New Mexico (1992–1994). Effect coefficients ($\bar{\beta}$) are averages across models in the indicated set. Bivariate plots between Mexican vole abundance and each of the highest ranked independent regressor variables are also shown (n = 42 combinations of site and year).

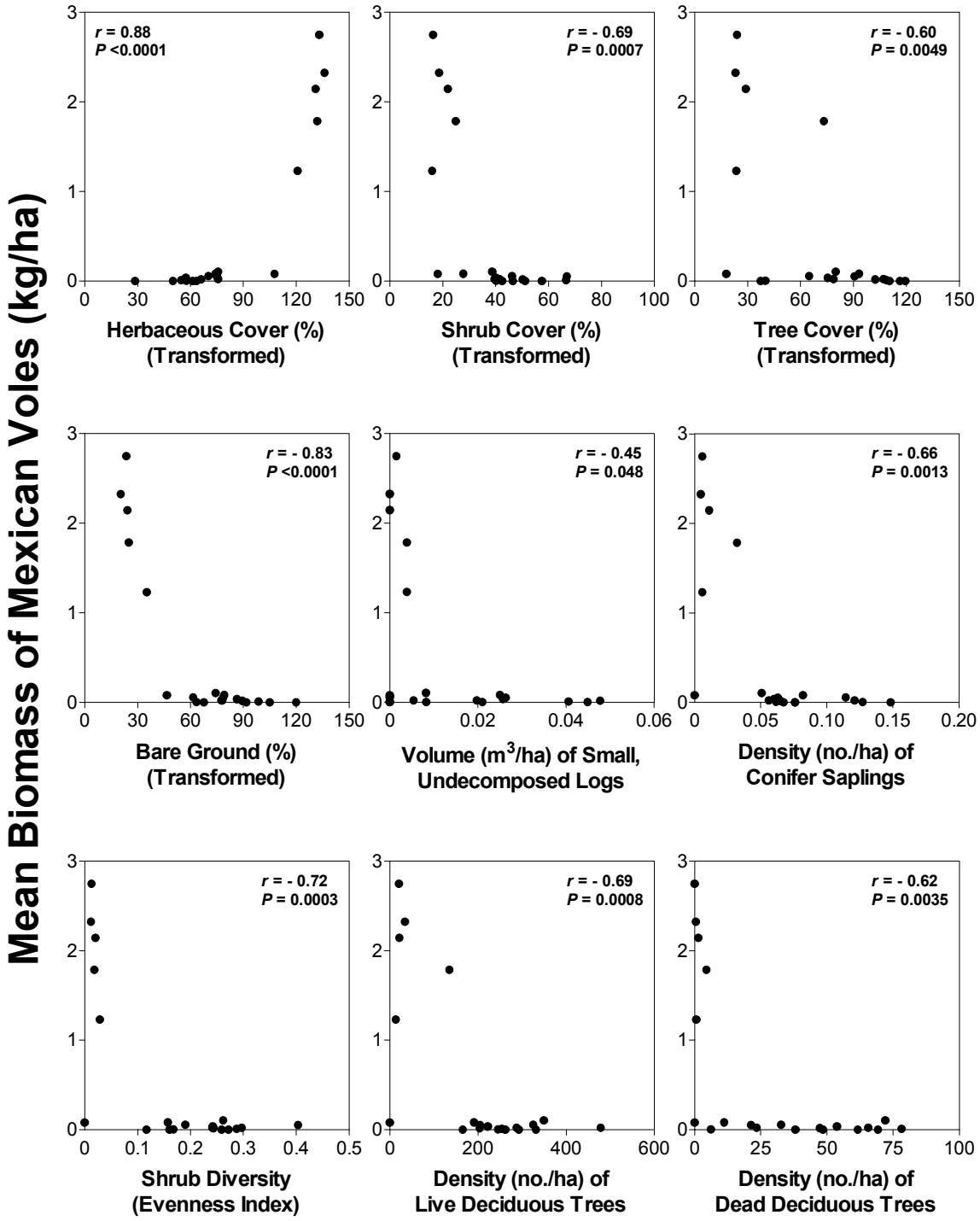

Figure 2.17. Additional correlations between Mexican vole abundance and selected microhabitat variables in the Sacramento Mountains, New Mexico (1991–1996).

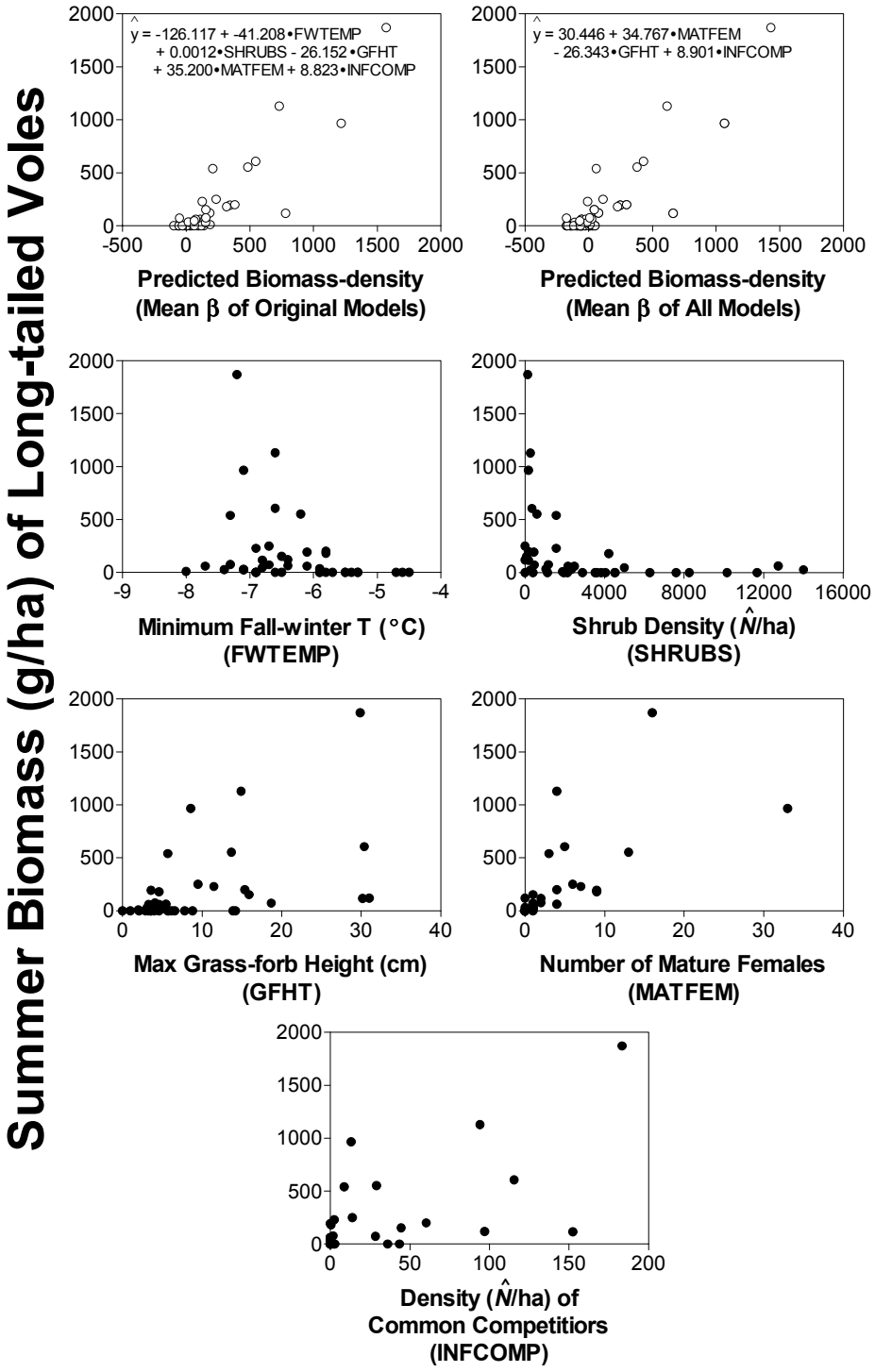

Figure 2.18. Fit of *a priori* (original) and all (original and exploratory) models predicting summer abundance of long-tailed voles from likely biotic and abiotic factors in the Sacramento Mountains, New Mexico (1992–1994). Effect coefficients ($\bar{\beta}$) are averages across models in the indicated set. Bivariate plots between long-tailed vole abundance and each of the highest ranked independent regressor variables are also shown (n = 42 combinations of site and year).

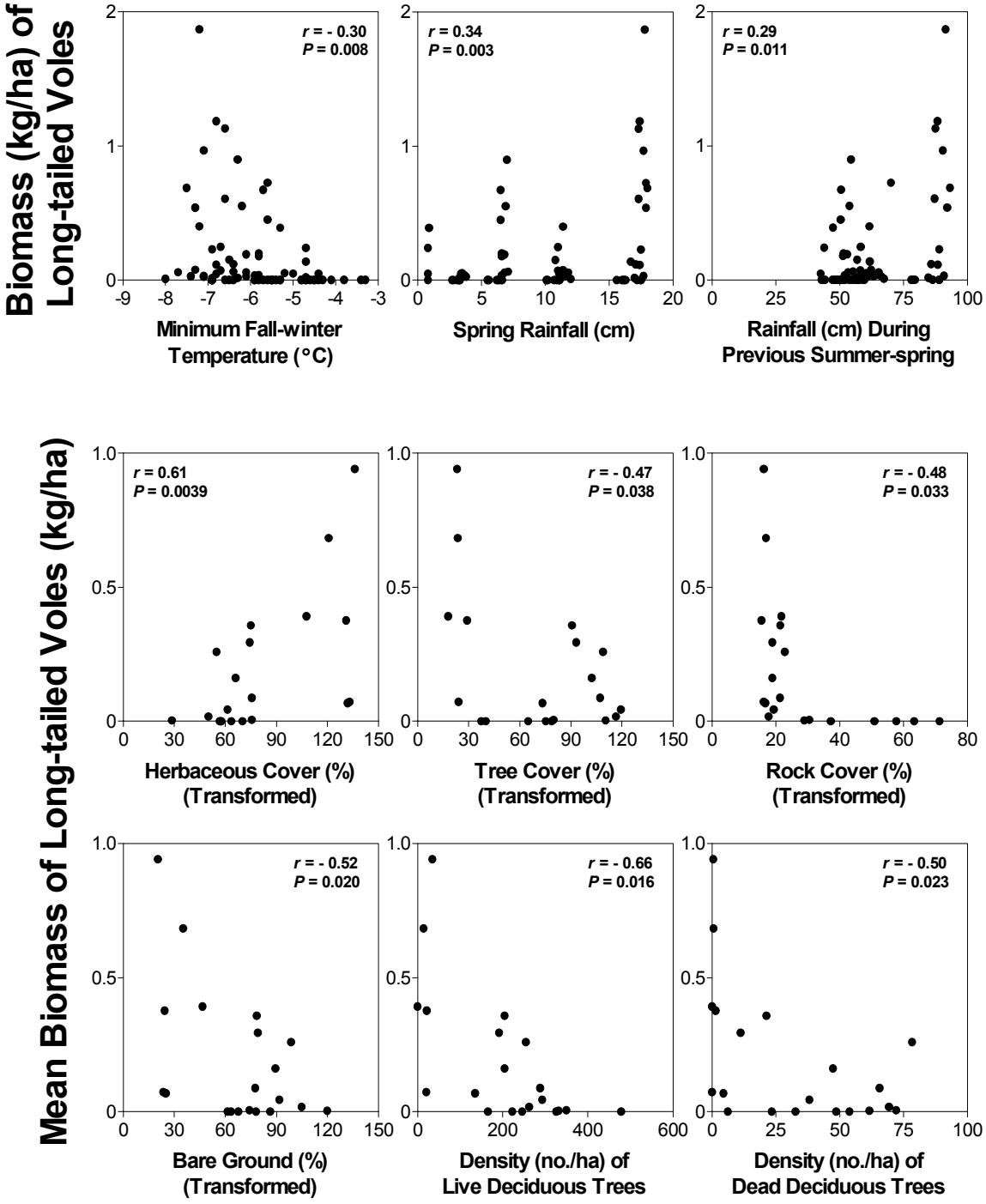

Figure 2.19. Additional correlations between long-tailed vole abundance and selected weather and microhabitat variables in the Sacramento Mountains, New Mexico (1991–1996).

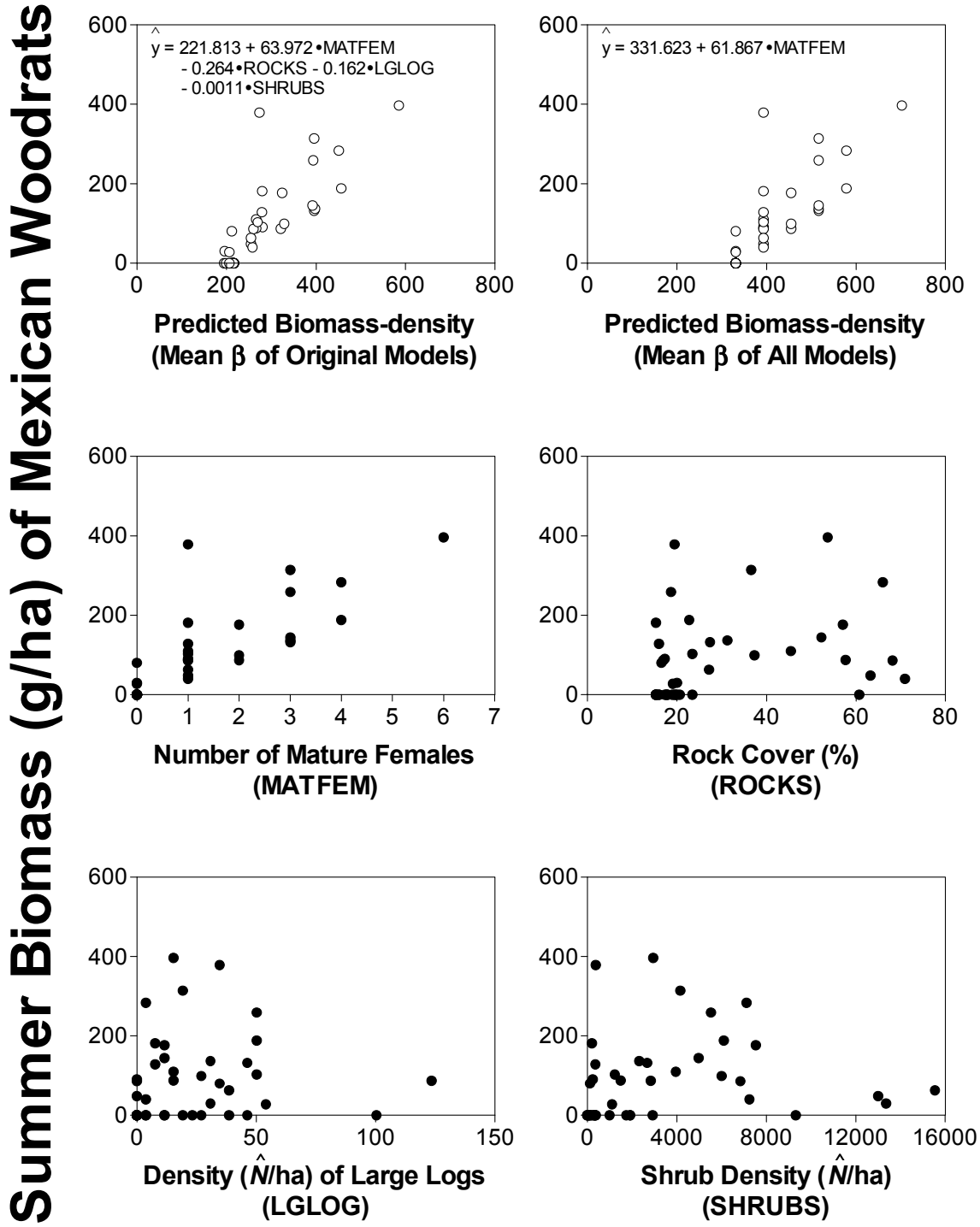

Figure 2.20. Fit of *a priori* (original) and all (original and exploratory) models predicting summer abundance of Mexican woodrats from likely biotic and abiotic factors in the Sacramento Mountains, New Mexico (1992–1994). Effect coefficients ($\bar{\beta}$) are averages across models in the indicated set. Bivariate plots between Mexican woodrat abundance and each of the highest ranked independent regressor variables are also shown (n = 42 combinations of site and year).

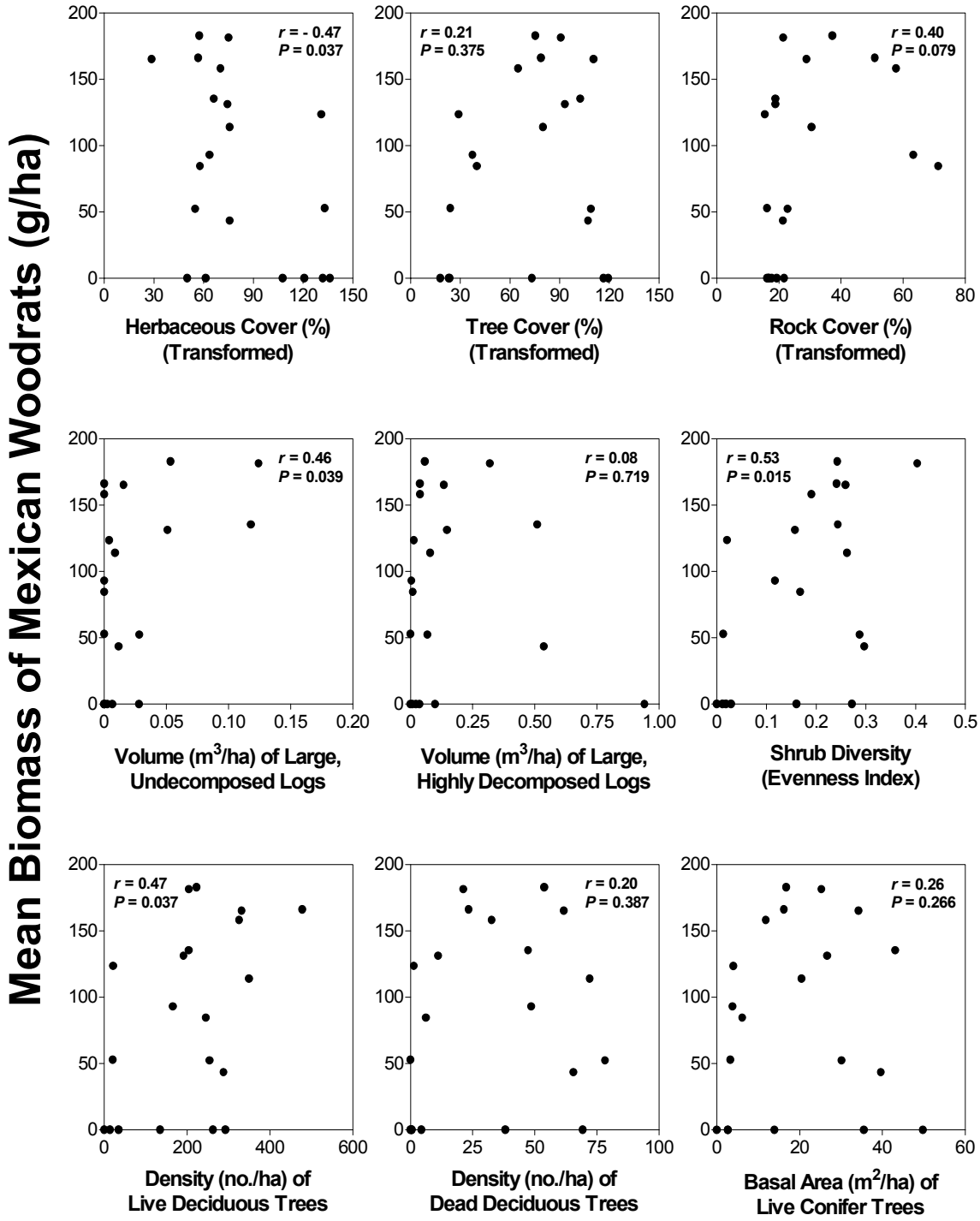

Figure 2.21. Additional correlations between Mexican woodrat abundance and selected microhabitat variables in the Sacramento Mountains, New Mexico (1991–1996).

APPENDIX 2.A
Estimation of Weather Parameters

During development of *a priori* models, several weather variables were identified as key factors that could influence rodent abundance. These variables included, cumulative rainfall (cm) during two consecutive spring and summers (April–August) preceding the summer that rodent abundance was sampled (PREVRAIN), average minimum temperatures (°C) during late fall and winter months (November–February) prior to the summer sampling of abundance (FWTEMP), cumulative rainfall during spring (March–May) preceding sampling of abundance (RSPRAIN), and cumulative rainfall during a previous summer through to the spring (July–May) immediately preceding sampling of abundance (PSSRAIN). The modeling approach used in this study required site- and time- specific observations for these variables. Although precipitation categories and minimum and maximum temperatures were recorded at each grid during periods of small-mammal trapping, these data were not sufficient. Rather, I input expected weather values given the elevation (m) of each site (taken at the center point of each trapping grid) and a predictive equation. In this appendix, I describe the procedures used to estimate the expected weather values.

I developed the predictive equations retrospectively from data recorded at nine weather stations (Table 2.A.1). I modeled the relationship between each weather variable and elevation of the weather station using simple linear regression. I used the least squares method to estimate intercept and slope coefficients (Table 2.A.2). All relationships were statistically significant (P of all F-tests ranged 0.0001–0.03) except for the relationship of RSPRAIN in 1994 and 1996 ($P = 0.14$). Excepting these two cases, the amount of variation explained by each significant relationship was moderately high (R^2 ranged 0.55–0.88). Coefficients of variation for slope parameters ranged 14 to 37% (Table 2.A.2). Despite the moderate level of precision, I considered the expected weather values sufficient because these values would be used to identify relative importance among key factors rather than predicting precise estimates of rodent abundance. I also assumed that estimation of unconditional variances for parameters of the rodent-abundance models would be large enough to account for variation associated with estimating the weather variables. Unconditional variance includes uncertainty associated with variation in model structure that can result when different data are analyzed in addition to variation associated with model parameter estimates (Burnham and Anderson 1998).

APPENDIX 2.A (Continued).

Table 2.A.1. Weather stations from which data were compiled and analyzed to estimate expected precipitation and temperature values given elevations in the Sacramento Mountains, New Mexico.

Name	Number [a]	LAT	LONG [b]	Elevation (m)
Alamogordo	290199	32 53	105 57	1326
Tularosa	299165	33 05	106 03	1351
Picacho 2 WSW	296804	33 21	105 10	1537
Carizozo	291515	33 39	105 53	1652
Elk 2	292865	32 57	105 18	1747
Capitan	291440	33 33	105 34	1976
Mountain Park	295960	32 57	105 51	2070
Cloudcroft 2	291931	32 57	105 44	2640
Sunspot Observatory	–	32 47	105 49	2798

[a] National Oceanic and Atmospheric Administration, Cooperative Station number.

[b] Latitude and longitude given as degrees and minutes.

APPENDIX 2.A (Continued).

Table 2.A.2. Coefficients and statistics describing fit of simple linear models used to predict selected weather values from elevation (m) in the Sacramento Mountains, New Mexico. Model form is $Y = \beta_0 + \beta_1 \cdot$ elevation.

Dependent Variable [a]	Year	*n*	β_0	β_1	CV[β_1] (%)	*P* of > *F*-test[c]	R^2
PREVRAIN	1991	9	−4.317	0.0283	28.1	0.0093	0.64
PREVRAIN	1992	9	−5.185	0.0315	19.2	0.0013	0.79
PREVRAIN	1993	9	2.778	0.0280	20.9	0.0020	0.76
PREVRAIN	1994	9	4.423	0.0265	27.5	0.0084	0.65
PREVRAIN	1995	9	−3.340	0.0270	26.1	0.0065	0.68
PREVRAIN	1996	9	−7.541	0.0246	25.5	0.0058	0.69
FWTEMP	1991	8 [b]	4.243	−0.0039	35.9	0.0318	0.56
FWTEMP	1992	8 [b]	4.972	−0.0047	26.5	0.0094	0.70
FWTEMP	1993	8 [b]	4.756	−0.0042	30.7	0.0175	0.64
FWTEMP	1994	8 [b]	3.088	−0.0040	36.6	0.0340	0.55
FWTEMP	1995	8 [b]	7.354	−0.0048	21.9	0.0038	0.78
FWTEMP	1996	8 [b]	5.866	−0.0041	32.4	0.0208	0.62
RSPRAIN	1991	9	−5.511	0.0049	30.8	0.0147	0.60
RSPRAIN	1992	9	7.134	0.0041	35.4	0.0257	0.53
RSPRAIN	1993	9	−2.214	0.0035	36.0	0.0271	0.52
RSPRAIN	1994	9	3.029	0.0032	60.0	0.1395 ns	0.28
RSPRAIN	1995	9	−1.491	0.0019	26.8	0.0074	0.66
RSPRAIN	1996	9	−0.226	0.0004	57.5	0.1449 ns	0.28
PSSRAIN	1991	9	−18.645	0.0352	14.6	0.0002	0.87
PSSRAIN	1992	9	4.989	0.0332	13.8	0.0002	0.88
PSSRAIN	1993	9	−15.708	0.0267	14.8	0.0003	0.87
PSSRAIN	1994	9	−11.013	0.0279	20.5	0.0018	0.77
PSSRAIN	1995	9	−24.363	0.0323	18.3	0.0010	0.81
PSSRAIN	1996	9	−12.476	0.0219	20.2	0.0017	0.78

[a] Defined in text above.

[b] Data unavailable from Sunspot Observatory, New Mexico.

[c] ns–non-significant at $\alpha = 0.05$.

APPENDIX 2.B
Covariance Structure of Mixed Models

I used a repeated measures, mixed model to estimate the significance of temporal and spatial variation in biomass (g/ha) of five murid rodents. Use of this approach requires an assumption about the structure of sampling covariance. This appendix describes the criteria used to select among three common patterns in covariance, autoregressive (first order), compound symmetric, and unstructured. The figures below show the absolute values of temporal autocorrelations of biomass at 1, 2, and 3-year intervals. Autoregressive patterns should show decreases in r with time interval. Most of these data show the opposite pattern; values further in time are more correlated. This pattern is typical of data that demonstrate periodic cycles. I could not find a way to model this type of covariance structure and therefore deferred to use of the unstructured form which resulted in loss of degrees of freedom for testing the significance of temporal versus spatial effects on biomass. According to Akaike's Information Criterion, models with unstructured covariance provided the most likely model of abundance, relative to the three types of structure. The result was consistent among rodent species (Table 2.B.1).

Table 2.B.1. Comparison of repeated measures, mixed models used to quantify significance of time and space on biomass (g/ha) of five murid rodents assuming three forms of covariance structure.

	Akaike's Information Criterion (AIC)			
Species	Autoregressive First Order	Compound Symmetric	Unstructured	Likelihood Ratio Test [a]
Deer mouse	-166.500	-164.780	-159.310	26.94 *
Brush mouse	-173.944	-173.317	-155.647	51.34 *
Mexican vole	-234.267	-231.037	-195.461	87.15 *
Long-tailed vole	-198.802	-199.603	-176.454	60.70 *
Mexican woodrat	-174.699	-173.434	-170.375	22.13 *

[a] Calculated as (-2 log Likelihood $_{\text{reduced model}}$ − -2 log Likelihood $_{\text{unstructured}}$), where the reduced model was the one with the next highest AIC values, and compared to χ^2 distribution with 2 df ($\alpha = 0.05$);
* Indicates that a model with unstructured covariances provided a significantly better fit to the data.

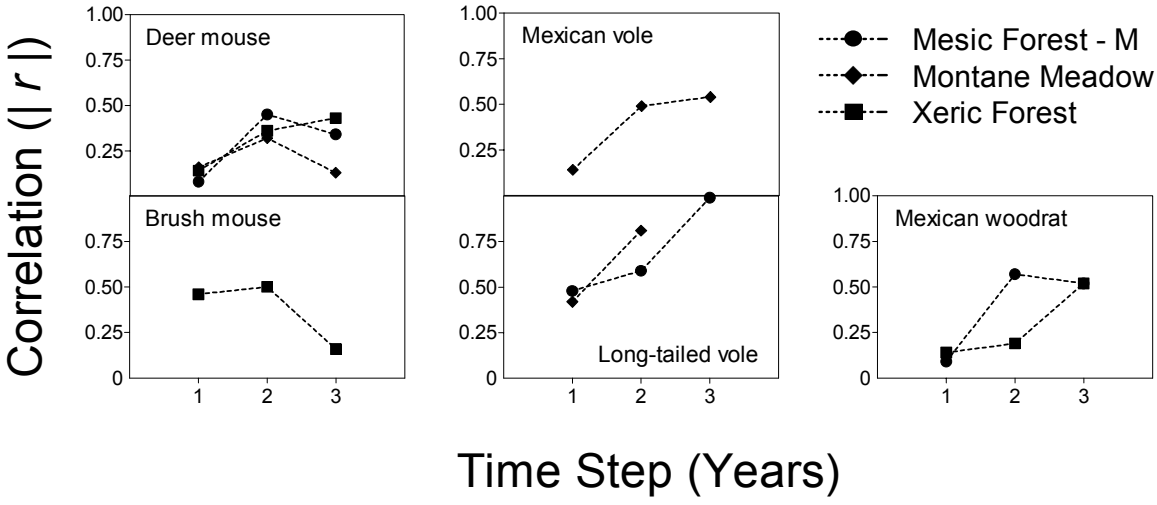

Figure 2.B.1. Autocorrelation of biomass (g/ha) of five rodent species in the Sacramento Mountains, New Mexico (1992–1995) over different time intervals.

APPENDIX 2.C
Mammal Captures

Several species of small and medium-sized mammals were captured using live-traps in three broad habitat types of the Sacramento Mountains, New Mexico during 1991–1996. Only species targeted for study were given individual marks. Values below (Table 2.C.1) are combined over seasons and site replicates. Total checks of large and extra-large Sherman traps (morning and afternoon) were as follows: late-seral mesic forest (10,921), mid-seral mesic forest (63,730), montane meadow (42,840), xeric forest (69,225). Individuals identified to genus only (91 captures) are not listed.

Table 2.C.1. Captures of small and medium-sized mammals (1991–1996) in the Sacramento Mountains, New Mexico.

	Captures by Habitat Type [a]												
Order / Family[b]	Late-seral Mesic Forest			Mid-seral Mesic Forest			Montane Meadow			Xeric Forest			
Species	N	P	R	N	P	R	N	P	R	N	P	R	Total N
Insectivora / Soricidae													
Sorex monticolus	99	—	—	186	—	—	103	—	—	1	—	—	389
S. nanus	1	—	—	3	—	—	—	—	—	—	—	—	4
S. merriami	2	—	—	23	—	—	6	—	—	—	—	—	32
Lagomorpha / Leporidae													
Sylvilagus robustus	—	—	—	—	—	—	1	—	—	—	—	—	1
S. auduboni	—	—	—	—	—	—	—	—	—	1	—	—	1

APPENDIX 2.C. (Table 2.C.1. Continued).

Order / Family Species	Captures by Habitat Type [a]												
	Late-seral Mesic Forest			Mid-seral Mesic Forest			Montane Meadow			Xeric Forest			
	N	P	R	N	P	R	N	P	R	N	P	R	Total N
Rodentia / Sciuridae													
*Tamias canipes**	56	13	83	267	30	507	34	2	22	120	48	273	477
*T. minimus atristriatus**	7	0	5	19	0	65	2	0	1	20	2	41	48
Spermophilus variegatus	—	—	—	6	—	—	—	—	—	7	—	—	13
Tamiasciurus hudsonicus	12	—	—	92	—	—	—	—	—	16	—	—	120
/ Geomyidae													
Thomomys bottae	—	—	—	1	—	—	13	—	—	—	—	—	14
/ Muridae													
*Reithrodontomys megalotis**	—	—	—	—	—	—	—	—	—	2	0	0	2
*Peromyscus maniculatus**	194	1	461	1394	61	2574	428	4	687	725	70	1792	2741
*P. boylii**	1	0	0	57	3	128	0	0	0	747	90	1873	805
*P. nasutus**	—	—	—	1	0	0	—	—	—	—	—	—	1
*Neotoma albigula**	—	—	—	—	—	—	—	—	—	5	0	6	5
*N. mexicana**	18	2	41	113	20	301	14	0	12	165	14	288	310
*Microtus mexicanus**	5	0	3	76	0	31	2001	65	1669	163	3	143	2245
*M. longicaudus**	82	0	173	568	2	911	406	1	615	2	0	3	1058
/ Zapodidae													
*Zapus hudsonius**	—	—	—	—	—	—	3	0	1	—	—	—	3

APPENDIX 2.C. (Table 2.C.1. Continued).

Order / Family Species	Captures by Habitat Type [a]												
	Late-seral Mesic Forest			Mid-seral Mesic Forest			Montane Meadow			Xeric Forest			
	N	P	R	N	P	R	N	P	R	N	P	R	Total N
Carnivora / Mustelidae													
Mustela frenata	—	—	—	2	—	—	—	—	—	1	—	—	3
/ Mephitidae													
Spilogale gracilis	—	—	—	22	—	—	—	—	—	—	—	—	22
Mephitis mephitis	—	—	—	—	—	—	—	—	—	5	—	—	5

[a] N = number of individuals if the species was ear-tagged (*) or total captures of unmarked species; P = number of captures of animals marked in previous trapping session; R = number of recaptures of marked animals during a trapping session. Zeros are shown only when individuals were marked originally and thus there was opportunity to record previous or recaptures. Dashes indicate that no individuals were ear-tagged and therefore previous captures or recaptures could not be detected.

[b] Nomenclature follows Jones et al. (1997).

APPENDIX 2.D.
Density Estimates

Density ($\hat{N}$/ha), population size ($\hat{N}$), mean maximum distance moved (MMDM in m), and the probability of capture ($\hat{p}$) of five murid rodents estimated from live-trapping data collected in the southern Sacramento Mountains, New Mexico during 1991–1996 and using various closed-population estimators (M) in Program CAPTURE (Rexstad and Burnham 1991). Standard errors are shown in parentheses.

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
PEMA	SUM/91	MF	BLUF	60.9	(4.56)	290	(21.0)	27	(3.9)	0.19	201	Mh
PEMA	SUM/92	MF	DELW	6.8	(0.89)	40	(3.0)	52	(14.5)	0.45	38	Mh
PEMA	SUM/93	MF	DELW	3.3	(0.90)	24	(3.8)	85	(34.9)	0.22	21	Mb
PEMA	FAL/93	MF	DELW	1.1	(0.30)	5	(1.2)	13	(14.9)	0.28	4	Mh
PEMA	WIN/94	MF	DELW	4.4	(1.97)	26	(7.4)	48	(45.1)	0.10	13	Mh
PEMA	SPR/94	MF	DELW	2.6	(0.69)	15	(2.9)	40	(22.3)	0.39	14	Mth
PEMA	SUM/94	MF	DELW	20.5	(5.07)	105	(23.9)	26	(11.1)	0.09	55	Mtb
PEMA	SUM/95	MF	DELW	5.4	(0.82)	35	(3.0)	57	(17.0)	0.46	34	Mh
PEMA	SUM/96	MF	DELW	15.1	(2.03)	94	(9.5)	51	(11.5)	0.34	72	Mh
PEMA	SUM/91	MF	GRES	38.8	(3.73)	196	(17.0)	30	(5.7)	0.17	137	Mh
PEMA	SUM/92	MF	HAYC	7.9	(2.99)	51	(15.7)	56	(29.5)	0.12	25	Mth
PEMA	SUM/93	MF	HAYC	3.8	(0.71)	28	(1.7)	73	(25.2)	0.31	27	Mb
PEMA	FAL/93	MF	HAYC	2.1	(0.41)	11	(0.4)	30	(22.9)	0.45	11	Mb
PEMA	WIN/94	MF	HAYC	4.2	(0.94)	27	(3.9)	60	(23.7)	0.20	24	Mtb
PEMA	SPR/94	MF	HAYC	5.0	(1.70)	32	(7.6)	63	(35.1)	0.15	17	Mh
PEMA	SUM/94	MF	HAYC	11.3	(2.45)	80	(12.5)	68	(21.0)	0.20	48	Mh
PEMA	SUM/95	MF	HAYC	5.2	(0.97)	36	(3.8)	65	(21.2)	0.40	31	Mh
PEMA	SUM/92	MF	LWIL	1.0	(0.45)	8	(1.6)	80	(56.8)	0.27	8	Mbh
PEMA	SUM/93	MF	LWIL	2.0	(0.64)	15	(2.3)	73	(38.8)	0.25	13	Mh
PEMA	SUM/92	MF	WAYL	7.4	(1.42)	48	(6.7)	69	(20.0)	0.20	40	Mb
PEMA	SUM/93	MF	WAYL	4.5	(2.80)	35	(20.7)	80	(25.8)	0.16	27	Mtb

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
PEMA	SUM/94	MF	WAYL	12.9	(1.16)	78	(3.1)	49	(10.4)	0.22	76	Mbh
PEMA	SUM/92	MF	WIWH	4.3	(1.15)	27	(5.0)	51	(24.7)	0.23	21	Mth
PEMA	SUM/93	MF	WIWH	4.4	(1.07)	31	(5.2)	73	(26.1)	0.20	26	Mb

PEMA	SUM/94	MF	WIWH	7.4	(1.74)	44	(8.3)	45	(17.9)	0.16	30	Mth
PEMA	SUM/92	MF	ZINK	1.4	(0.47)	7	(0.5)	72	(48.3)	0.50	7	Mbh
PEMA	SUM/93	MF	ZINK	3.8	(3.16)	29	(22.9)	79	(39.9)	0.09	16	Mb
PEMA	SUM/94	MF	ZINK	11.9	(5.89)	78	(37.7)	59	(18.0)	0.09	42	Mb
PEMA	SUM/95	MF	ZINK	2.7	(0.69)	17	(2.7)	51	(25.4)	0.45	16	Mh
PEMA	SUM/92	MM	DELW	17.0	(4.38)	48	(8.7)	27	(12.9)	0.14	23	Mh
PEMA	SUM/93	MM	DELW	3.2	(0.78)	8	(0.7)	19	(14.5)	0.31	8	Mo
PEMA	FAL/93	MM	DELW	1.7	(----)	3	(---)	--	(---)	----	3	
PEMA	WIN/94	MM	DELW	1.1	(----)	2	(---)	--	(---)	----	2	
PEMA	SPR/94	MM	DELW	2.2	(1.17)	9	(1.9)	58	(45.4)	0.25	7	Mh
PEMA	SUM/94	MM	DELW	6.5	(1.49)	18	(2.3)	29	(14.0)	0.30	16	Mth
PEMA	SUM/95	MM	DELW	11.2	(2.60)	26	(5.0)	14	(7.9)	0.20	19	Mh
PEMA	SUM/96	MM	DELW	16.4	(2.93)	49	(3.8)	31	(11.7)	0.24	42	Mo
PEMA	SUM/92	MM	HAYC	0.9	(0.29)	3	(0.7)	42	(19.6)	0.25	3	Mo
PEMA	SUM/93	MM	HAYC	0.6	(----)	1	(---)	--	(---)	----	1	
PEMA	SUM/94	MM	HAYC	1.5	(0.77)	6	(1.0)	52	(41.3)	0.38	6	Mth
PEMA	SUM/95	MM	HAYC	0.7	(0.66)	3	(0.5)	65	(94.0)	0.31	3	Mo
PEMA	SUM/92	MM	LWIL	11.1	(2.78)	36	(4.6)	37	(16.5)	0.26	29	Mh
PEMA	SUM/93	MM	LWIL	5.5	(2.33)	23	(4.9)	59	(33.9)	0.24	18	Mh
PEMA	SUM/94	MM	LWIL	10.2	(2.84)	43	(6.6)	62	(22.2)	0.20	36	Mb
PEMA	SUM/92	MM	WAYL	10.3	(3.09)	32	(7.5)	33	(13.9)	0.15	25	Mb
PEMA	SUM/93	MM	WAYL	8.9	(2.09)	29	(3.8)	38	(15.2)	0.25	24	Mh
PEMA	SUM/94	MM	WAYL	42.9	(8.94)	122	(21.5)	27	(7.8)	0.15	57	Mh
PEMA	SUM/92	MM	WILL	4.4	(2.09)	17	(2.0)	52	(40.6)	0.22	15	Mo
PEMA	SUM/93	MM	WILL	2.6	(1.71)	14	(1.6)	84	(70.4)	0.24	13	Mo
PEMA	SUM/94	MM	WILL	10.6	(7.92)	37	(25.8)	43	(21.2)	0.25	20	Mbh
PEMA	SUM/95	MM	WILL	4.3	(0.97)	11	(0.9)	20	(13.6)	0.31	11	Mo
PEMA	SUM/92	MM	WIWH	6.5	(1.92)	22	(2.1)	40	(22.2)	0.37	21	Mth
PEMA	SUM/93	MM	WIWH	3.4	(0.91)	8	(0.9)	15	(15.0)	0.28	8	Mo
PEMA	SUM/94	MM	WIWH	5.2	(2.15)	25	(2.1)	72	(41.2)	0.22	22	Mt
PEMA	SUM/94	OF	GDSL	10.5	(1.46)	63	(6.0)	48	(13.2)	0.32	51	Mh

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
PEMA	SUM/95	OF	GDSL	4.0	(1.01)	27	(4.2)	62	(27.2)	0.35	22	Mh
PEMA	SUM/96	OF	GDSL	9.9	(1.44)	64	(6.3)	56	(14.3)	0.37	52	Mh
PEMA	SUM/94	OF	SUNS	11.4	(2.28)	69	(11.5)	47	(14.1)	0.23	45	Mh
PEMA	SUM/95	OF	SUNS	3.1	(0.52)	22	(0.3)	68	(23.1)	0.51	22	Mh
PEMA	SUM/92	XF	CARR	4.7	(1.18)	23	(5.0)	22	(14.3)	0.17	16	Mh
PEMA	SUM/93	XF	CARR	0.7	(0.21)	4	(0.1)	48	(40.7)	0.56	4	Mo
PEMA	SUM/94	XF	CARR	2.3	(0.37)	12	(0.9)	31	(17.3)	0.31	12	Mo
PEMA	SUM/95	XF	CARR	4.2	(0.99)	23	(4.1)	36	(19.0)	0.26	18	Mth
PEMA	SUM/92	XF	DRYB	8.4	(1.11)	47	(4.3)	47	(13.1)	0.44	45	Mh
PEMA	SUM/93	XF	DRYB	3.6	(0.89)	24	(4.2)	66	(25.6)	0.21	21	Mb
PEMA	SUM/94	XF	DRYB	4.9	(1.27)	41	(6.6)	97	(32.6)	0.40	31	Mh
PEMA	SUM/95	XF	DRYB	2.6	(0.46)	17	(0.6)	56	(22.7)	0.48	17	Mth
PEMA	SUM/91	XF	FIRE	2.4	(0.71)	18	(2.4)	83	(39.4)	0.34	15	Mh
PEMA	SUM/92	XF	FIRE	9.4	(1.06)	59	(3.1)	51	(13.0)	0.28	55	Mb
PEMA	SUM/93	XF	FIRE	1.6	(0.57)	13	(0.6)	85	(51.7)	0.36	13	Mo
PEMA	FAL/93	XF	FIRE	1.6	(0.64)	10	(1.8)	48	(44.7)	0.26	9	Mo
PEMA	WIN/94	XF	FIRE	3.2	(0.72)	16	(3.0)	32	(16.9)	0.25	14	Mh

PEMA	SPR/94	XF	FIRE	2.0	(0.40)	11	(1.1)	37	(21.3)	0.27	11	Mo
PEMA	SUM/94	XF	FIRE	1.3	(0.42)	8	(0.9)	44	(37.1)	0.29	8	Mo
PEMA	SUM/92	XF	JAMS	3.5	(0.81)	21	(3.0)	58	(25.8)	0.34	19	Mh
PEMA	SUM/93	XF	JAMS	3.1	(0.77)	23	(3.3)	74	(29.1)	0.48	21	Mh
PEMA	FAL/93	XF	JAMS	10.8	(2.92)	57	(11.8)	34	(22.0)	0.11	23	Mh
PEMA	WIN/94	XF	JAMS	6.7	(1.10)	36	(3.5)	42	(17.0)	0.18	30	Mt
PEMA	SPR/94	XF	JAMS	7.4	(3.47)	42	(19.6)	42	(14.7)	0.13	29	Mtb
PEMA	SUM/94	XF	JAMS	12.2	(1.78)	65	(7.9)	35	(10.3)	0.24	49	Mh
PEMA	SUM/95	XF	JAMS	3.3	(0.59)	22	(0.3)	67	(24.9)	0.51	22	Mo
PEMA	SUM/96	XF	JAMS	10.3	(2.05)	63	(11.0)	48	(12.3)	0.19	49	Mb
PEMA	SUM/91	XF	SIXT	8.0	(3.75)	56	(25.6)	71	(22.3)	0.08	33	Mb
PEMA	SUM/92	XF	TRAL	8.1	(1.54)	52	(7.6)	55	(16.3)	0.19	43	Mb
PEMA	SUM/93	XF	TRAL	9.3	(1.26)	57	(5.0)	51	(13.6)	0.38	48	Mth
PEMA	SUM/94	XF	TRAL	12.0	(6.07)	70	(35.8)	47	(14.8)	0.09	38	Mb
PEMA	SUM/92	XF	WALK	2.3	(0.66)	18	(2.7)	83	(36.9)	0.40	18	Mh
PEMA	SUM/93	XF	WALK	0.7	(0.28)	4	(1.0)	44	(40.6)	0.27	4	Mbh
PEMA	SUM/94	XF	WALK	2.4	(1.61)	14	(8.7)	40	(26.3)	0.13	10	Mb

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
PEMA	SUM/95	XF	WALK	0.3	(----)	1	(---)	--	(---)	----	1	
PEBO	SUM/91	MF	GRES	5.2	(0.84)	26	(3.1)	37	(14.9)	0.18	24	Mbh
PEBO	SUM/92	MF	HAYC	1.7	(1.36)	11	(8.4)	53	(22.3)	0.06	5	Mo
PEBO	SUM/93	MF	HAYC	1.0	(0.56)	7	(1.9)	69	(70.0)	0.23	5	Mh
PEBO	FAL/93	MF	HAYC	0.5	(0.22)	3	(1.3)	53	(22.3)	0.14	2	Mh
PEBO	WIN/94	MF	HAYC	0.3	(----)	1	(---)	--	(---)	----	1	
PEBO	SPR/94	MF	HAYC	0.3	(----)	1	(---)	--	(---)	----	1	
PEBO	SUM/94	OF	SUNS	0.3	(----)	1	(---)	--	(---)	----	1	
PEBO	SUM/92	XF	CARR	23.2	(2.21)	130	(9.1)	37	(7.9)	0.28	103	Mh
PEBO	SUM/93	XF	CARR	5.0	(0.91)	34	(3.0)	64	(22.0)	0.44	32	Mh
PEBO	SUM/94	XF	CARR	6.5	(1.05)	37	(4.6)	40	(12.9)	0.25	34	Mtb
PEBO	SUM/95	XF	CARR	3.7	(0.91)	26	(3.5)	67	(28.9)	0.38	23	Mh
PEBO	SUM/92	XF	DRYB	4.7	(0.50)	25	(0.9)	31	(11.9)	0.36	25	Mo
PEBO	SUM/93	XF	DRYB	4.4	(1.00)	30	(4.8)	62	(21.7)	0.21	26	Mb
PEBO	SUM/94	XF	DRYB	1.7	(0.36)	11	(0.1)	58	(29.2)	0.61	11	Mo
PEBO	SUM/95	XF	DRYB	2.0	(0.71)	18	(2.8)	101	(49.8)	0.33	15	Mth
PEBO	SUM/91	XF	FIRE	2.3	(0.59)	15	(1.4)	76	(35.4)	0.28	15	Mbh
PEBO	SUM/92	XF	FIRE	5.9	(1.16)	38	(4.6)	55	(20.8)	0.28	31	Mh
PEBO	SUM/93	XF	FIRE	7.7	(1.39)	55	(6.8)	70	(18.8)	0.37	46	Mb
PEBO	FAL/93	XF	FIRE	2.1	(1.06)	13	(6.3)	51	(18.7)	0.12	7	Mo
PEBO	WIN/94	XF	FIRE	7.4	(1.15)	32	(4.6)	17	(9.0)	0.16	26	Mo
PEBO	SPR/94	XF	FIRE	4.4	(0.86)	24	(2.8)	52	(21.6)	0.30	21	Mth
PEBO	SUM/94	XF	FIRE	11.8	(1.36)	66	(5.3)	37	(10.0)	0.27	55	Mh
PEBO	SUM/92	XF	JAMS	7.9	(1.09)	45	(3.6)	45	(14.5)	0.36	41	Mbh
PEBO	SUM/93	XF	JAMS	3.9	(1.43)	20	(5.7)	26	(25.7)	0.10	14	Mt
PEBO	FAL/93	XF	JAMS	3.4	(0.47)	16	(0.6)	39	(16.7)	0.47	16	Mo
PEBO	WIN/94	XF	JAMS	2.4	(0.71)	12	(2.8)	40	(26.0)	0.25	10	Mth
PEBO	SPR/94	XF	JAMS	1.9	(1.02)	12	(5.6)	66	(46.8)	0.15	9	Mh
PEBO	SUM/94	XF	JAMS	2.1	(0.49)	12	(0.4)	50	(30.0)	0.42	12	Mo
PEBO	SUM/95	XF	JAMS	0.6	(0.15)	3	(0.0)	27	(29.8)	0.58	3	Mth

PEBO	SUM/96	XF	JAMS	3.2	(0.74)	20	(2.6)	58	(26.2)	0.48	19	Mh
PEBO	SUM/91	XF	SIXT	1.3	(----)	5	(---)	--	(---)	----	5	

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
PEBO	SUM/93	XF	TRAL	0.3	(----)	1	(---)	--	(---)	----	1	
PEBO	SUM/94	XF	TRAL	0.3	(----)	1	(---)	--	(---)	----	1	
PEBO	SUM/92	XF	WALK	15.3	(1.40)	84	(5.5)	35	(7.7)	0.36	72	Mh
PEBO	SUM/93	XF	WALK	10.8	(2.56)	69	(14.5)	56	(15.4)	0.15	50	Mb
PEBO	SUM/94	XF	WALK	16.4	(3.04)	92	(15.1)	39	(11.0)	0.22	45	Mh
PEBO	SUM/95	XF	WALK	4.2	(1.00)	30	(4.5)	69	(26.1)	0.40	26	Mh
MIME	SUM/91	MF	BLUF	6.8	(2.48)	35	(11.1)	38	(27.2)	0.03	8	Mh
MIME	SUM/92	MF	DELW	13.2	(4.11)	63	(17.5)	19	(15.7)	0.03	14	Mh
MIME	SUM/95	MF	DELW	0.3	(----)	1	(---)	--	(---)	----	1	
MIME	SUM/96	MF	DELW	0.5	(----)	2	(---)	--	(---)	----	2	
MIME	SUM/91	MF	GRES	0.5	(----)	1	(---)	--	(---)	----	1	
MIME	SUM/92	MF	WAYL	0.8	(----)	3	(---)	--	(---)	----	3	
MIME	SUM/94	MF	WAYL	0.3	(----)	1	(---)	--	(---)	----	1	
MIME	SUM/92	MF	WIWH	2.6	(1.33)	17	(2.1)	57	(66.2)	0.15	16	Mbh
MIME	SUM/92	MF	ZINK	6.4	(2.53)	36	(11.8)	38	(27.2)	0.02	11	Mh
MIME	SUM/93	MF	ZINK	0.5	(----)	2	(---)	--	(---)	----	2	
MIME	SUM/95	MF	ZINK	1.5	(----)	5	(0.8)	--	(---)	0.15	5	Mo
MIME	SUM/92	MM	DELW	152.5	(15.99)	356	(30.2)	16	(4.0)	0.08	217	Mth
MIME	SUM/93	MM	DELW	60.2	(4.32)	134	(6.4)	15	(3.4)	0.21	122	Mbh
MIME	FAL/93	MM	DELW	9.6	(3.59)	17	(0.8)	21	(24.8)	0.25	17	Mtb
MIME	WIN/94	MM	DELW	38.1	(10.61)	79	(20.5)	8	(5.7)	0.04	25	Mh
MIME	SPR/94	MM	DELW	3.4	(1.31)	8	(1.4)	15	(21.2)	0.12	7	Mo
MIME	SUM/94	MM	DELW	36.1	(3.32)	82	(5.9)	16	(3.8)	0.13	71	Mth
MIME	SUM/95	MM	DELW	162.9	(12.79)	365	(26.9)	15	(2.2)	0.09	244	Mh
MIME	SUM/96	MM	DELW	82.1	(12.11)	190	(25.4)	15	(4.1)	0.08	107	Mth
MIME	SUM/92	MM	HAYC	97.1	(12.47)	240	(26.0)	19	(4.6)	0.07	143	Mth
MIME	SUM/93	MM	HAYC	43.5	(3.74)	109	(6.0)	20	(4.4)	0.11	91	Mo
MIME	FAL/93	MM	HAYC	34.7	(11.30)	62	(16.4)	8	(13.0)	0.03	16	Mh
MIME	WIN/94	MM	HAYC	10.6	(3.08)	20	(6.9)	15	(5.4)	0.06	8	Mh
MIME	SPR/94	MM	HAYC	11.4	(1.18)	21	(2.1)	1	(1.4)	0.13	19	Mo
MIME	SUM/94	MM	HAYC	44.5	(4.54)	111	(7.0)	20	(5.3)	0.10	89	Mo
MIME	SUM/95	MM	HAYC	54.7	(6.88)	111	(12.4)	10	(4.1)	0.06	71	Mo
MIME	SUM/92	MM	LWIL	94.2	(18.52)	222	(32.2)	18	(8.9)	0.04	87	Mh

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
MIME	SUM/93	MM	LWIL	16.6	(5.71)	39	(13.0)	15	(5.4)	0.02	8	Mh
MIME	SUM/94	MM	LWIL	14.0	(3.50)	33	(5.4)	21	(13.2)	0.11	24	Mh
MIME	SUM/92	MM	WAYL	183.4	(18.15)	390	(37.0)	10	(2.0)	0.06	220	Mth
MIME	SUM/93	MM	WAYL	29.1	(3.37)	63	(6.0)	14	(4.6)	0.09	49	Mo

MIME	SUM/94	MM	WAYL	18.9	(3.48)	49	(6.8)	21	(8.0)	0.12	37	Mth
MIME	SUM/92	MM	WILL	8.7	(3.16)	17	(6.1)	8	(7.5)	0.05	11	Mo
MIME	SUM/94	MM	WILL	1.8	(0.86)	4	(1.4)	11	(18.4)	0.17	3	Mh
MIME	SUM/92	MM	WIWH	115.7	(20.21)	270	(43.9)	15	(4.3)	0.05	118	Mh
MIME	SUM/93	MM	WIWH	71.5	(14.02)	184	(30.5)	22	(7.2)	0.05	82	Mh
MIME	SUM/94	MM	WIWH	28.4	(5.04)	70	(10.7)	19	(6.0)	0.09	48	Mth
MIME	SUM/96	OF	GDSL	1.9	(0.50)	7	(2.0)	7	(9.4)	0.09	5	Mh
MIME	SUM/92	XF	DRYB	2.9	(0.99)	16	(4.3)	41	(27.6)	0.10	12	Mh
MIME	SUM/91	XF	FIRE	0.3	(----)	1	(---)	--	(---)	----	1	
MIME	SUM/92	XF	FIRE	0.3	(----)	1	(---)	--	(---)	----	1	
MIME	SUM/92	XF	JAMS	7.5	(1.19)	33	(4.8)	12	(7.6)	0.09	25	Mo
MIME	FAL/93	XF	JAMS	1.0	(0.12)	3	(0.1)	20	(13.0)	0.84	3	Mbh
MIME	WIN/94	XF	JAMS	0.5	(----)	1	(---)	--	(---)	----	1	
MIME	SPR/94	XF	JAMS	0.3	(----)	1	(---)	--	(---)	----	1	
MIME	SUM/91	XF	SIXT	5.3	(1.10)	21	(4.5)	8	(7.3)	0.11	15	Mh
MIME	SUM/92	XF	TRAL	12.3	(1.10)	59	(3.3)	23	(8.2)	0.13	52	Mt
MIME	SUM/93	XF	TRAL	1.2	(0.42)	5	(1.9)	20	(13.0)	0.10	5	Mh
MIME	SUM/92	XF	WALK	6.1	(0.71)	26	(2.3)	14	(8.9)	0.12	23	Mo
MIME	SUM/93	XF	WALK	2.5	(1.36)	12	(6.4)	20	(13.0)	0.03	3	Mh
MIME	SUM/94	XF	WALK	0.3	(----)	1	(---)	--	(---)	----	1	
MILO	SUM/91	MF	BLUF	25.3	(13.21)	105	(54.1)	33	(41.1)	0.03	25	Mo
MILO	SUM/92	MF	DELW	26.1	(3.31)	120	(15.2)	22	(5.0)	0.09	92	Mtb
MILO	SUM/93	MF	DELW	6.7	(1.73)	36	(8.5)	38	(15.5)	0.09	28	Mb
MILO	FAL/93	MF	DELW	1.7	(0.28)	8	(0.8)	17	(14.6)	0.42	8	Mo
MILO	WIN/94	MF	DELW	0.5	(----)	1	(---)	--	(---)	----	1	
MILO	SPR/94	MF	DELW	0.5	(----)	1	(---)	--	(---)	----	1	
MILO	SUM/94	MF	DELW	0.5	(----)	2	(---)	--	(---)	----	2	
MILO	SUM/95	MF	DELW	1.4	(0.42)	7	(0.4)	53	(38.7)	0.23	7	Mo
MILO	SUM/96	MF	DELW	6.9	(1.19)	31	(5.0)	33	(13.0)	0.14	27	Mtb

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
MILO	SUM/91	MF	GRES	3.7	(1.01)	10	(5.1)	33	(12.4)	0.08	6	Mo
MILO	SUM/94	MF	HAYC	0.3	(----)	1	(---)	--	(---)	----	1	
MILO	WIN/94	MF	HAYC	0.3	(----)	1	(---)	--	(---)	----	1	
MILO	SUM/92	MF	LWIL	1.3	(----)	5	(1.9)	--	(---)	0.10	3	Mh
MILO	SUM/93	MF	LWIL	2.0	(1.00)	11	(5.3)	33	(12.4)	0.04	4	Mh
MILO	SUM/92	MF	WAYL	21.8	(2.50)	103	(10.7)	30	(7.9)	0.11	77	Mth
MILO	SUM/93	MF	WAYL	1.9	(0.60)	12	(1.1)	50	(38.7)	0.18	12	Mb
MILO	SUM/94	MF	WAYL	0.7	(0.50)	4	(2.7)	33	(12.4)	0.06	3	Mo
MILO	SUM/92	MF	WIWH	6.9	(0.75)	34	(2.0)	25	(10.6)	0.15	32	Mo
MILO	SUM/93	MF	WIWH	1.2	(0.38)	6	(1.4)	25	(25.3)	0.18	5	Mh
MILO	SUM/92	MF	ZINK	33.8	(10.89)	164	(56.8)	31	(7.7)	0.05	87	Mb
MILO	SUM/93	MF	ZINK	5.6	(0.94)	31	(2.5)	55	(20.3)	0.25	28	Mth
MILO	SUM/94	MF	ZINK	1.2	(0.39)	5	(1.4)	22	(25.2)	0.16	4	Mh
MILO	SUM/95	MF	ZINK	0.5	(----)	2	(---)	--	(---)	----	2	
MILO	SUM/92	MM	DELW	4.1	(0.68)	9	(0.7)	10	(8.4)	0.18	9	Mo
MILO	SUM/93	MM	DELW	5.6	(1.01)	13	(0.3)	19	(11.7)	0.38	13	Mbh
MILO	SPR/94	MM	DELW	1.5	(0.35)	4	(0.3)	22	(14.6)	0.23	4	Mo
MILO	SUM/96	MM	DELW	1.1	(----)	2	(---)	--	(---)	----	2	

MILO	SUM/92	MM	HAYC	3.3	(2.83)	11	(5.4)	39	(55.8)	0.05	6 Mo
MILO	SUM/94	MM	HAYC	5.7	(2.96)	15	(7.1)	22	(14.6)	0.04	4 Mh
MILO	SUM/92	MM	LWIL	32.9	(26.44)	59	(52.9)	6	(3.6)	0.04	26 Mbh
MILO	SUM/93	MM	LWIL	20.5	(5.07)	58	(11.6)	27	(10.1)	0.14	38 Mh
MILO	SUM/94	MM	LWIL	7.8	(3.90)	28	(7.6)	54	(39.4)	0.10	17 Mh
MILO	SUM/92	MM	WAYL	54.0	(9.65)	140	(20.3)	23	(7.3)	0.06	78 Mh
MILO	SUM/93	MM	WAYL	16.5	(1.74)	37	(1.2)	20	(6.6)	0.20	36 Mo
MILO	SUM/94	MM	WAYL	13.9	(2.38)	36	(4.2)	21	(8.2)	0.17	31 Mh
MILO	SUM/92	MM	WILL	13.7	(2.88)	22	(5.3)	9	(5.8)	0.08	15 Mh
MILO	SUM/93	MM	WILL	27.5	(16.44)	70	(40.9)	20	(8.5)	0.05	36 Mbh
MILO	SUM/94	MM	WILL	1.9	(0.59)	3	(0.8)	8	(13.0)	0.13	3 Mo
MILO	SUM/95	MM	WILL	2.6	(0.71)	5	(0.5)	14	(15.8)	0.19	5 Mo
MILO	SUM/92	MM	WIWH	19.7	(7.02)	56	(17.9)	27	(11.1)	0.07	37 Mb
MILO	SUM/93	MM	WIWH	12.8	(6.57)	46	(17.3)	51	(32.5)	0.06	14 Mh
MILO	SUM/94	MM	WIWH	1.8	(0.63)	4	(0.9)	11	(15.8)	0.13	4 Mo

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
MILO	SUM/94	OF	GDSL	1.9	(0.46)	10	(1.2)	28	(23.8)	0.14	9	Mo
MILO	SUM/95	OF	GDSL	1.2	(0.55)	5	(0.4)	61	(62.3)	0.21	5	Mo
MILO	SUM/96	OF	GDSL	12.4	(1.52)	64	(6.2)	40	(10.7)	0.21	52	Mth
MILO	SUM/94	OF	SUNS	0.3	(----)	1	(---)	--	(---)	----	1	
MILO	SUM/95	OF	SUNS	0.8	(0.26)	4	(0.1)	48	(40.4)	0.32	4	Mo
MILO	SUM/92	XF	TRAL	0.5	(----)	2	(---)	--	(---)	----	2	
NEME	SUM/92	MF	DELW	3.1	(1.20)	18	(5.3)	41	(31.0)	0.17	8	Mh
NEME	SUM/93	MF	DELW	0.5	(0.23)	3	(0.2)	34	(48.6)	0.42	3	Mo
NEME	SUM/95	MF	DELW	0.6	(0.42)	4	(1.4)	52	(74.4)	0.41	3	Mth
NEME	SUM/96	MF	DELW	0.8	(0.41)	5	(1.1)	70	(64.7)	0.29	5	Mbh
NEME	SUM/91	MF	GRES	0.9	(0.78)	6	(1.9)	86	(127.8)	0.13	4	Mh
NEME	SUM/92	MF	HAYC	1.7	(0.78)	11	(1.2)	59	(61.2)	0.21	10	Mo
NEME	SUM/93	MF	HAYC	1.2	(0.41)	9	(0.9)	80	(49.0)	0.46	9	Mth
NEME	FAL/93	MF	HAYC	2.2	(1.38)	13	(4.1)	46	(70.2)	0.11	8	Mh
NEME	WIN/94	MF	HAYC	0.8	(0.09)	5	(0.1)	53	(15.3)	0.60	5	Mbh
NEME	SPR/94	MF	HAYC	0.5	(0.28)	3	(0.1)	50	(74.3)	0.85	3	Mbh
NEME	SUM/94	MF	HAYC	0.9	(0.21)	5	(0.0)	35	(27.8)	0.35	5	Mth
NEME	SUM/95	MF	HAYC	1.4	(0.37)	9	(0.4)	51	(32.9)	0.41	9	Mo
NEME	SUM/92	MF	WAYL	0.7	(0.34)	4	(1.4)	40	(41.8)	0.28	4	Mh
NEME	SUM/93	MF	WAYL	0.3	(----)	1	(---)	--	(---)	----	1	
NEME	SUM/94	MF	WAYL	0.6	(0.38)	4	(0.2)	60	(84.8)	0.44	4	Mo
NEME	SUM/92	MF	WIWH	0.7	(0.35)	4	(1.4)	36	(40.6)	0.20	4	Mh
NEME	SUM/93	MF	WIWH	0.3	(----)	1	(---)	--	(---)	----	1	
NEME	SUM/92	MF	ZINK	0.9	(0.40)	6	(1.4)	67	(57.0)	0.36	6	Mh
NEME	SUM/93	MF	ZINK	2.3	(0.66)	16	(3.0)	65	(29.5)	0.20	14	Mbh
NEME	SUM/94	MF	ZINK	1.5	(0.32)	9	(0.2)	48	(27.9)	0.47	9	Mo
NEME	SUM/95	MF	ZINK	1.4	(0.30)	8	(0.3)	42	(26.3)	0.44	8	Mo
NEME	SUM/92	MM	DELW	0.6	(----)	1	(---)	--	(---)	----	1	
NEME	FAL/93	MM	DELW	0.6	(----)	1	(---)	--	(---)	----	1	
NEME	SUM/96	MM	DELW	2.0	(1.01)	7	(3.1)	44	(20.4)	0.14	5	Mo
NEME	SUM/92	MM	WIWH	1.1	(----)	2	(---)	--	(---)	----	2	
NEME	SUM/93	MM	WIWH	0.6	(----)	1	(---)	--	(---)	----	1	

APPENDIX 2.D. (Continued).

Species[a]	Seas./Yr	Hab.[b]	Site[c]	Density		$\hat{N}$		MMDM		$\hat{p}$[d]	N_M[e]	M[f]
NEME	SUM/94	MM	WIWH	1.1	(0.33)	4	(0.6)	44	(20.4)	0.28	4	Mo
NEME	SUM/94	OF	GDSL	0.9	(0.31)	5	(0.4)	34	(39.1)	0.35	5	Mo
NEME	SUM/95	OF	GDSL	0.5	(0.37)	4	(0.5)	79	(102.6)	0.31	4	Mo
NEME	SUM/96	OF	GDSL	1.9	(0.31)	10	(0.5)	27	(17.5)	0.41	11	Mo
NEME	SUM/92	XF	CARR	2.6	(0.92)	17	(3.6)	56	(37.1)	0.16	14	Mh
NEME	SUM/93	XF	CARR	0.5	(----)	2	(---)	--	(---)	----	2	
NEME	SUM/95	XF	CARR	0.3	(0.27)	4	(0.0)	172	(175.6)	0.88	4	Mbh
NEME	SUM/92	XF	DRYB	3.3	(0.48)	18	(0.3)	35	(17.6)	0.50	18	Mb
NEME	SUM/93	XF	DRYB	1.0	(0.63)	7	(2.7)	72	(74.3)	0.34	5	Mth
NEME	SUM/94	XF	DRYB	0.5	(----)	2	(---)	--	(---)	----	2	
NEME	SUM/95	XF	DRYB	0.8	(0.35)	6	(0.5)	81	(64.8)	0.33	6	Mo
NEME	SUM/91	XF	FIRE	1.0	(----)	4	(---)	--	(---)	----	4	
NEME	SUM/92	XF	FIRE	0.3	(0.22)	2	(1.4)	65	(34.8)	0.10	2	Mh
NEME	SUM/93	XF	FIRE	1.0	(0.51)	8	(2.3)	88	(64.8)	0.26	8	Mo
NEME	FAL/93	XF	FIRE	0.3	(----)	1	(---)	--	(---)	----	1	
NEME	WIN/94	XF	FIRE	0.4	(0.30)	2	(1.4)	34	(48.6)	0.25	2	Mh
NEME	SUM/94	XF	FIRE	1.2	(0.49)	6	(1.8)	20	(28.3)	0.17	5	Mo
NEME	SUM/92	XF	JAMS	1.6	(0.63)	11	(2.5)	61	(42.5)	0.21	9	Mh
NEME	SUM/93	XF	JAMS	2.3	(0.65)	14	(2.4)	45	(27.3)	0.35	11	Mh
NEME	FAL/93	XF	JAMS	1.2	(0.78)	6	(0.1)	61	(89.2)	0.67	6	Mb
NEME	WIN/94	XF	JAMS	0.3	(----)	1	(---)	--	(---)	----	1	
NEME	SUM/94	XF	JAMS	0.9	(0.35)	5	(1.9)	65	(34.8)	0.10	3	Mh
NEME	SUM/95	XF	JAMS	0.8	(0.29)	5	(0.4)	44	(41.7)	0.38	5	Mo
NEME	SUM/96	XF	JAMS	2.1	(0.32)	11	(0.3)	31	(17.8)	0.51	11	Mo
NEME	SUM/91	XF	SIXT	0.4	(0.11)	3	(0.0)	65	(34.8)	0.86	3	Mbh
NEME	SUM/92	XF	TRAL	1.2	(0.41)	9	(1.2)	82	(48.2)	0.33	9	Mh
NEME	SUM/93	XF	TRAL	1.1	(0.41)	8	(0.1)	77	(56.3)	0.49	8	Mtb
NEME	SUM/94	XF	TRAL	0.5	(0.30)	4	(0.3)	73	(78.9)	0.38	4	Mo
NEME	SUM/92	XF	WALK	0.6	(0.39)	4	(2.5)	65	(34.8)	0.09	3	Mo
NEME	SUM/93	XF	WALK	1.7	(1.44)	16	(5.8)	108	(121.5)	0.12	6	Mh
NEME	SUM/94	XF	WALK	1.1	(0.43)	7	(0.5)	57	(53.2)	0.36	7	Mo
NEME	SUM/95	XF	WALK	1.7	(0.31)	9	(0.4)	30	(20.5)	0.39	9	Mo

APPENDIX 2.D. (Continued).

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[a] Species acronyms are PEMA–deer mouse, PEBO–brush mouse, MIME–Mexican vole, MILO–long-tailed vole, NEME–Mexican woodrat.

[b] Habitat codes are MF–mid-seral mesic forest, MM–montane meadow, OF–late-seral mesic forest, XF–xeric forest.

[c] Site codes and UTM (E, N), zone 13, locations are BLUF–Bluff Springs (4303, 36321), CARR–Carr Gap (4547, 36438), DELW–Delworth (MF: 4309, 36330; MM: 4305, 36324), DRYB–Dry Burnt Canyon (4473, 36458), FIRE-91–Fire (4552, 36450), FIRE-92 (4547, 36446), GDSL–Goodsell (4322 , 36411), GRES–Greasy Canyon (4418, 36328), HAYC–Hay Canyon (MF: 4396, 36295; MM: 4393, 36298), JAMS–James (4447, 36474), LWIL–Lower Wills Canyon (MF: 4338, 36311; MM: 4331, 36311), SIXT–Sixteen Springs (4541, 36491), SUNS–Sunspot (4239, 36288), TRAL–Trail Canyon (4444, 36215), WALK–Walker (4521, 36474), WAYL–Wayland (MF: 4375, 36237, MM: 4375, 36239), WILL–Upper Wills Canyon (4304, 36293), WIWH–Willie White Canyon (MF: 4322, 36324, MM: 4313, 36323), ZINK–Zink Trick (4372, 36513).

[d] Point estimates of $\hat{p}$ for models Mo, Mb, and Mh, otherwise given as an average of $\hat{p}_j$.

[e] Number of individuals marked + unmarked mortalities.

[f] Model codes are o–all individuals have the same and constant *p*, b–behavioral reaction to initial capture, h-individual reaction to capture (e.g. age- or sex-specific differences), and t-time related capture.

APPENDIX 2.E
Movement Patterns

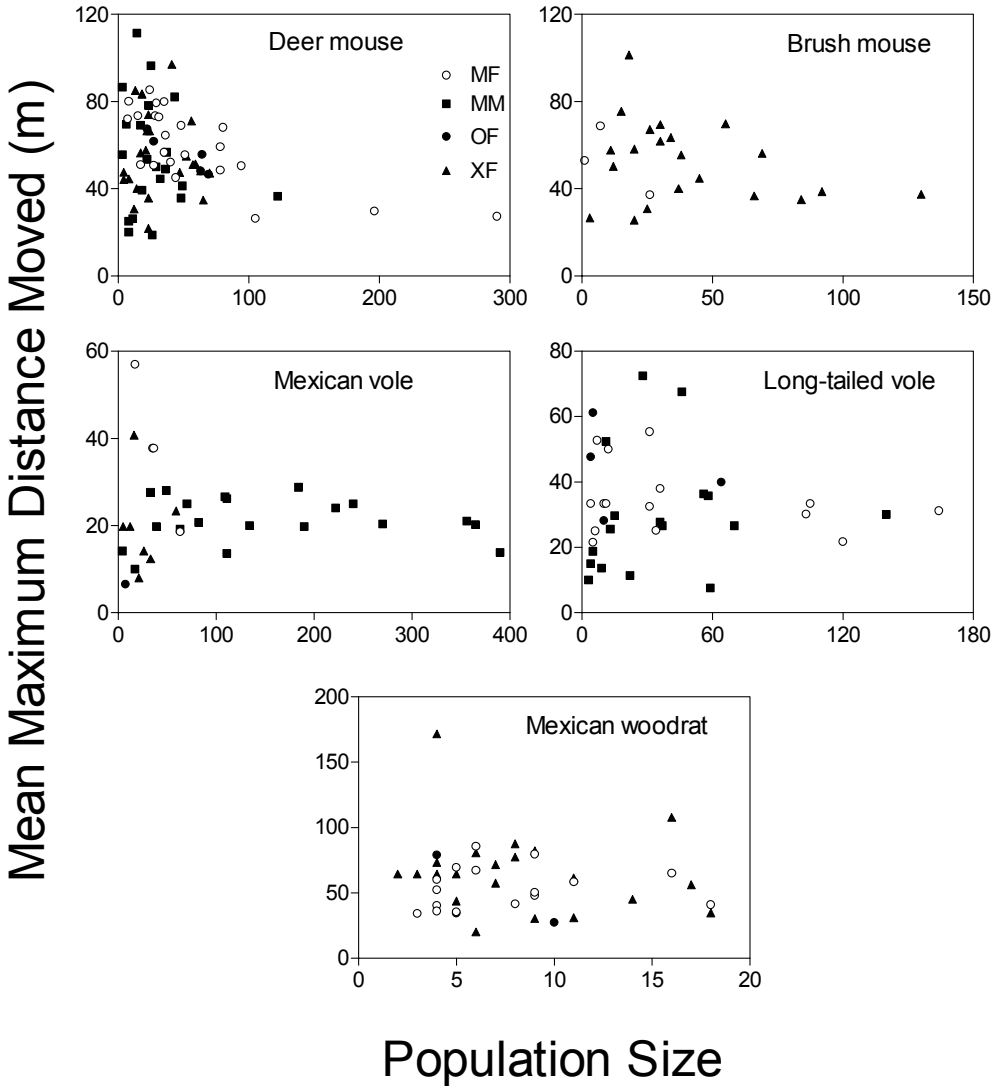

Figure 2.E.1. Movements of five murid rodents as a function of population size ($\hat{N}$) in the Sacramento Mountains, New Mexico during six summers (July–August,1991–1996). Each graph point represents a single population in a given summer. Habitat codes are as follows: MF–mid-seral mesic forest, MM–montane meadow, OF–late-seral mesic forest, XF–xeric forest. Habitat symbols are consistent for all graphs.

CHAPTER 3

FUNCTIONAL AND REPRODUCTIVE RESPONSES BY MEXICAN SPOTTED OWLS

Prey availability is a prominent factor that affects predator populations. Accordingly, ecologists have developed a plethora of models to describe and predict interactions between predators and their prey (Royama 1971, Chesson 1978, Berryman 1992). Specific predictions of predator-prey theory, however, rarely evolve into strategies for conserving endangered predators. This may in part stem from overly simplistic assumptions invoked when modeling these theories (see discussions by Solomon 1949 and Murdoch and Briggs 1996). For conservation, the utility of predator-prey theory may stem from analysis of associated assumptions rather than reliance on derived predictions.

There are two functions that are fundamental to models of predator-prey dynamics, the functional and numerical responses of a predator to its prey. Functional responses describe the amount of prey a predator will consume given the prey's abundance (Solomon 1949). Numerical responses describe the change in a predators' numbers following change in prey abundance (Solomon 1949). Reciprocal influence of a predator on abundance of its prey depends on both responses (Holling 1959, Jedrzejewski et al. 1996). Mathematical functions used to describe either response can take a number of forms depending on the type and behavior of the predator and its prey (Holling 1959,

Murdoch and Oaten 1975, Abrams 1982, Fujii et al. 1986). Quantifying functional and numerical responses directly may therefore provide basic information for conserving specific predators and for refining theoretical models (Cox 1993, Taylor 1994).

Prey selection and switching by a predator are also fundamental aspects of predator-prey theory. When quantified, these behaviors can also provide useful insight for conserving predators. Functional responses are demonstrably stronger to preferred prey (Murdoch 1969). When switching occurs, alternative prey are taken in disproportionately greater amounts as preferred prey become less available (Murdoch and Oaten 1975, Real 1990). If selection of preferred prey is disproportionately greater as its availability increases or disproportionately less as its availability decreases, then switching can theoretically promote stability within a predator-prey system (Murdoch and Oaten 1975). Quantifying prey selection and switching should therefore be useful when attempting to establish the relative influence of multiple prey species on a predator population and, hence, for identifying prey species to target in conservation efforts.

In this chapter, I focus on functional and reproductive (short-term numerical) responses of Mexican spotted owls (*Strix occidentalis lucida*) and discuss briefly how this information pertains to the owl's conservation. The Mexican spotted owl is a threatened species that occupies montane forests and canyons of the southwestern United States and portions of Mexico (USDI 1995). An understanding of how prey populations may specifically influence this owl species is considered paramount for its conservation (USDI 1995).

Much of our knowledge about the owl's relationships with its prey is limited primarily to description of food habits (Ward and Block 1995, Young et al. 1997,

Seamans and Gutiérrez 1999). For comparison, I first summarize the food habits for the study population occurring in the Sacramento Mountains, New Mexico, and identify prey commonly consumed during six consecutive breeding seasons. This is an expanded description of food habits for the same population provided previously by Ward and Block (1995). Second, I test for selection among common prey, quantify the owl's functional response, and test for prey switching by contrasting the owl's diet with measures of prey abundance previously described in Chapter 2. Combined, these analyses help to identify key prey species according to the owl's feeding behavior.

In addition, I quantify reproductive output in this spotted owl population as a function of prey abundance to document short-term numerical response. There are several reasons for treating reproductive output in this spotted owl population as a numerical response. First, the spatial aggregation of the Sacramento, Sierra Blanca, and Capitan Mountains is geographically isolated from other portions of this owl's breeding habitat (e.g., see Keitt et al. 1995). The nearest known location for breeding by Mexican spotted owls beyond this mountain complex is approximately 90 km. This distance is well beyond that observed between natal sites and settlement areas for juvenile emigrants and it approaches the maximum final distance (92 km) known for dispersing juveniles (Gutiérrez et al. 1996, Ganey et al. 1998, Willey and van Riper 2000). Further, recent analysis of genetic variation within and among populations of Mexican spotted owls indicates that, on average, only 1.6 immigrants per approximately 5 yrs are recruited and reproduce within a different population (Barrowclough et al. 1999). Thus, annual recruitment of spotted owls into the Sacramento Mountains from immigration is likely a rare event, particularly during the breeding season. Second, mortality and emigration are

also probably close to zero during the breeding period when environmental conditions are less demanding. Mortality or dispersal of adults appears greatest during winter periods, particularly following years of low prey abundance (Ganey et al. *in review*). Also, mortality of young is negligible prior to dispersal, which commences in September (Gutiérrez et al. 1995, Ganey et al. 1998, Willey and van Riper 2000). Because immigration, emigration, and mortality are rare events during the breeding season, numerical change during this time must come from reproduction. Here, I focus on this short-term numerical response as a way to identify key prey species that may influence population change of spotted owls in the Sacramento Mountains.

Terms

Several terms found in this chapter have received wide and sometimes inconsistent use in the ecological literature. For clarity, I define key terms and pertinent authorities. Here, I follow Johnson (1980) for describing resource selection. Accordingly, *selection* is defined as the act of choosing a resource component (in this case, prey) and is demonstrated when that resource is used disproportionately given its availability. When prey use is disproportionately greater than its availability, I will refer to it as *prey selection*. When prey use is disproportionately less than its availability, I will call it *prey avoidance*.

Preference reflects the probability of a food resource being chosen if offered on an equal basis with other foods, and occurs independent of food availability (Johnson 1980). Preference for food types can be influenced by a number of factors including the user's reproductive and physiological state, ambient temperature, and food quality (Ellis et al. 1976, Houston 1993). Thus, selection alone does not necessarily reveal preference.

The term *availability* is often misused or undefined (Hall et al. 1997). Johnson (1980) defines resource availability as that quantity of a component that is accessible to a user. For operational purposes, I offer a detailed definition of prey availability as it may apply to Mexican spotted owls below (Appendix 3.A).

Functional response, *prey switching*, and *numerical response* have been defined above. However, it is important to note that Solomon (1949) describes two forms of functional response, one regarding the rate of prey consumption (i.e., number per unit time) by an individual predator relative to the prey's abundance and another describing the total numbers of prey consumed relative to the prey's abundance during a specific period. I will emphasize the latter.

Predictions

A priori predictions about a spotted owl's response to its prey can be formulated from existing knowledge of the owl's natural history. Spotted owls frequently consume great amounts of medium-sized rodents such as northern flying squirrels (*Glaucomys sabrinus*) and woodrats (*Neotoma* spp.) throughout much of their range (Gutiérrez et al. 1995). For example, these two rodents comprise 66% (median of 12 studies; Forsman et al. 1984, White 1996, Ward et al. 1998) and 76% (median of 8 studies; Verner et al. 1992, Smith et al. 1999) of prey biomass consumed by northern (*S. o. caurina*) and California spotted owls (*S. o. occidentalis*), respectively. In addition, northern spotted owls are known to select dusky-footed woodrats (*N. fuscipes*) over other prey and to select micro-habitats where this rodent is more available when hunting (Ward et al. 1998). Spotted owls that forage selectively for woodrats have smaller foraging areas, which appears to provide an energetic benefit (Zable et al. 1995, Ward et al. 1998). In

areas where woodrats are less available and flying squirrels are the primary prey, spotted owls expand their foraging range to encompass habitat where flying squirrels are more abundant (Carey et al. 1992, Zabel et al. 1995).

Similar responses by Mexican spotted owls are less apparent. Flying squirrels are not consumed because they generally do not co-occur with Mexican spotted owls (see ranges described for flying squirrels by Heaney 1999, Layne 1999). In addition, consumption of woodrats by the Mexican spotted owl follows a cline, being predominant in northwestern portions of its range and limited in southeastern portions (Ward and Block 1995:12). For example, woodrats comprise 76% (median for 7 studies summarized by Ward and Block 1995) of biomass consumed by Mexican spotted owls occurring in canyons of southern Utah compared to 23% (median for 2 studies summarized by Ward and Block 1995) in forested environments of the Sacramento Mountains, south-central New Mexico. Intermediate amounts of woodrats are consumed by Mexican spotted owls in central portions of its range. This pattern may in part be explained by the zoogeography of various woodrat species (Ward and Block 1995). As many as three species of woodrats (*N. cinerea*, *N. lepida*, and *N. mexicana*) may co-occur with Mexican spotted owls in southern Utah (Durrant 1952). Only one woodrat species (*N. mexicana*) is usually sympatric with spotted owls in the Sacramento Mountains (Findley et al. 1975).

Congruence between regional variation in woodrat distribution and diet of the Mexican spotted owl suggests that this owl's food habits may simply reflect availability rather than selection. If this is true, then tests for woodrat selection should be neutral (i.e., in accordance) with changes in its availability and the resulting functional response

of Mexican spotted owls in the Sacramento Mountain population should be similar to that of other non-selected prey. If these owls are not selective of any prey, and prey availabilities are asynchronous, then any switching behavior may be frequency-dependent and non-stabilizing.

Aspects of a raptor's natural and life history can also be used to predict the degree of specialized prey use (Steenhof and Kochert 1988). Specialization would be expected when (1) prey are stable and abundant; (2) distances from the owl's nest to its foraging sites are great; (3) the owl relies more on pursuit than on searching to capture prey; (4) difference among prey values are large and unambiguous.

Spotted owls forage over large areas and are central-place foragers but hunt by ambush following extended searches from elevated perches (Carey and Peeler 1995, Gutiérrez et al. 1995). Because their common prey are energetically similar per unit of mass (Graber 1962, Fleharty et al. 1973, Kaufman et al. 1975), prey value can be distinguished according to size, with woodrats being approximately 4 times larger than the next largest, common prey (Ward and Block 1995). If woodrats are found to be stable and abundant in the Sacramento Mountains, then three of the above conditions would be satisfied suggesting that spotted owls should show a moderate degree of specialization for woodrats. In this study, dietary selectivity would suggest behavioral specialization.

It is generally presumed that preference for a given food type by an organism is adopted because that behavior enhances fitness. Accordingly, I would expect that increases in abundance and use of preferred prey would be associated with increased reproductive success of spotted owls. Franklin et al. (2000) suspected that the distribution of woodrat habitat was linked to northern spotted owl reproductive output in

northwestern California. Moreover, Smith et al. (1999) found that consumption of dusky-footed woodrats was positively correlated with reproduction of spotted owls dwelling in southern California.. Hence, if I find a preference for woodrats by Mexican spotted owls in this study, I would also expect woodrat abundance to be positively correlated with the owl's reproductive output.

METHODS

Study Area

This study was conducted in the southern portion of the Sacramento Mountains of south-central New Mexico. Most of the study area was public land administered by the Sacramento Ranger District, Lincoln National Forest, USDA Forest Service (Fig. 3.1). The Sacramento Ranger District and associated in-holdings were approximately 2,223 km^2, of which 48% was presumed usable habitat for Mexican spotted owls (USDA Lincoln National Forest, *unpublished data*).

Elevations in the Sacramento Mountains ranged from 1300 m at the Tularosa Basin to a maximum of 2930 m at an unnamed summit east of Sunspot, New Mexico. Common soils included Cryoborolls, Argiborolls, Ustorthents, and Argiustolls (Ashford and Stury 1977). During the study period (1991–1996), annual precipitation ranged from 63 cm to 98 cm in Cloudcroft at 2652 m. Seasonally, about 60% of the annual precipitation occurred during July–September and coincided with warm temperatures. December and June temperatures averaged −0.4 °C and 14.0 °C, respectively. In general, weather during the study period was similar to that in previous years except that significantly less snow accumulated during late fall and winter months and slightly less

precipitation fell during summer monsoons (see study area descriptions in Chapters 1 and 2).

My research was confined to three broad "habitats" (*sensu* Hall et al. 1997) that were likely to be used by Mexican spotted owls or their prey and were categorized as mesic forest (MF), xeric forest (XF), or montane meadow (MM). I delineated these habitats according to broad vegetation associations (Dick-Peddie 1993), expected small mammal associations (Findley et al. 1975), and variation in environmental features (e.g., structural attributes of the vegetation, elevation, temperature) that could influence use of these habitats by the owl or its prey (Ganey and Dick 1995).

Vegetation in the mesic forest has been classified as Upper Montane Coniferous Forest by Moir (1993). This mixed-coniferous forest (>2280 m elevation) was dominated by Douglas-fir (*Psuedotsuga menziesii*) or white fir (*Abies concolor*). Vegetation in the xeric forest represented Lower Montane Coniferous Forest (2070–2590 m elevation) , and Coniferous Woodland (< 2070 m elevation; Moir 1993). Lower Montane Coniferous Forest was dominated by ponderosa pine (*Pinus ponderosa*). Conifer Woodlands were dominated by two-needle pinyon pine (*P. edulis*) or juniper (*Juniperus* spp.). Montane meadows included both the Montane Grassland described by USDA Forest Service (Lincoln National Forest Supervisor's Office, *unpublished data*) and wet meadows described by Dick-Peddie (1993). They occurred in valley bottoms >2130 m elevation and were comprised of monocotyledon and herbaceous dicotyledon plants (grasses and forbs), and scattered trees or shrubs along the periphery. This study area has been described further in Chapter 1 and by Kaufmann et al. (1998).

Sampling Design and Data Collection

Prey selection, functional response, and switching behavior may be quantified through controlled manipulation of prey abundance (e.g., Murdoch 1969) or through observational studies whereby predator behavior and prey abundance are sampled over long-enough time periods to witness variability in the latter (e.g., see Korpimäki and Norrdahl 1991). In this study, I used the observational approach. I therefore designed a sampling program to obtain estimates of prey consumption and owl reproduction over long enough periods to witness concordant changes in prey abundance. Accordingly, I sampled food habits and recorded number of spotted owl fledglings produced during consecutive breeding seasons from independent owl territories in the Sacramento Mountain population while sampling prey abundance at a spatial scale presumed to be concomitant with population processes of small mammals and the owl's foraging behavior.

Spotted owl diet. To quantify food habitats of Mexican spotted owls, I analyzed regurgitated pellets gathered opportunistically beneath spotted owl roosts and nests (Forsman et al. 1984, Marti 1987). For each set of pellets collected, the date of collection, owl territory identity or location, age and sex of owl that egested pellet (when actually observed), number and condition of pellets, and collector's name were recorded. Unless the condition of pellets at the time of collection indicated otherwise, I used the collection date to identify the reproductive period (breeding or non-breeding) during which these owls consumed the represented prey. Because pellets were difficult to find during the non-breeding period (1 October through 28/29 February) I only considered breeding season diets for analysis. Also, because I rarely knew if the pellets were

regurgitated by adult or juvenile spotted owls, I treated dietary data as samples of the amount of prey consumed by an entire spotted owl family during the breeding season that pellets were collected. These sampling procedures were conventional among all other studies of Mexican spotted owl food habits and therefore permitted comparison (Ward and Block 1995).

Spotted owl reproduction. I compiled information on the gender, age, and reproduction of Mexican spotted owls recorded during standardized surveys (USDA 1990, Ward and Salas 2000). Gender of spotted owls >1 yr of age was determined by pitch of calls. Calls made by males were lower in pitch (Forsman et al. 1984, Ganey 1990). Gender of juvenile owls could not be distinguished by call pitch and remained unknown. Roosting Mexican spotted owls 1, 2, and ≥3 yrs of age could be distinguished by visual inspection of their plumage through binoculars (Forsman 1981, Moen et al. 1991). However, it was unlikely that this method was used during all surveys (see Data Analysis). Thus, age was assigned according to two classes, young of the year (e.g., fledglings; owls <1 yr) or subadult and adult (≥1 yr). Nesting activity and number of fledglings produced per pair were determined by feeding mice to an individual subadult or adult owl during mid-April through mid-July and monitoring that owl's behavior (known as 'mousing'; Forsman 1983, Franklin et al. 1996). Absence of fledglings was inferred for a given year and pair if more than two mice were taken and then consumed, cached, or held for at least one hour by the same individual subadult or adult owl during the period when juveniles could normally be observed perched outside of the nest (Franklin et al. 1996, Seamans et al. 1999). Care, transport, and use of mice during this

research followed recently advocated protocols (National Academy of Sciences 1996, American Society of Mammalogists 1998).

Surveys conducted prior to mid-may that inferred non-nesting were usually followed by a second survey prior to August to verify reproductive status. During breeding seasons of 1993 and 1994 breeding status was also inferred from repeated observation of a small number of radio-marked individuals ($n \leq 14$ spotted owls studied by Ganey et al. *in review*) during the breeding season, in lieu of the mousing technique. Surveys were conducted in a different subset of owl territories each year with few territories being sampled during consecutive years (see Results). These subsets were not selected randomly. However, the spatial pattern of each set of surveyed territories did not show any atypical clustering compared to the distribution of all known territories and therefore appeared to provide a representative sample in each year.

Prey availability. I defined prey availability as the amount of common prey that could be accessed by parental spotted owls during the period when young were being raised (mid-May through August; Gutiérrez et al. 1995). Resource availability has typically been defined in similar, general terms (Johnson 1980, Manly et al. 1993, Hall et al. 1997). Frequently, abundance or a related index estimated without consideration of accessibility has been substituted for prey availability (Hutto 1990, Petty 1999). However, an investigator's choice of what constitutes “available” can greatly influence inferences about resource selection (see Appendix 3.A). Following its general definition, availability should impart both abundance and accessability of a resource to the focal predator (Johnson 1980).

Quantifying abundance of prey is relatively straightforward and unbiased estimators are well documented. However, quantifying access to prey by a focal predator is operationally problematic. Here, I considered the amount of common prey occurring in a spotted owl's foraging range accessible to that owl during the stage of predation that entails hunting for prey and therefore as a coarse level of prey availability (Appendix 3.A). Therefore, available prey in this study comprised a subset of the prey's abundance within the entire study area and that subset was defined according to the predator's habitat choice at an appropriate spatial scale. Johnson (1980) has argued that selection of food by an organism is a hierarchical process following selection of living space and feeding sites within that space. My definition of availability incorporates the former process but not the latter. This definition can lead to a more conservative test for selection of undetectable prey (Appendix 3.A).

I quantified this coarse level of prey availability by converting biomass of a given prey per unit of area (g/ha) to biomass (g) in an owl's foraging range. I used the following steps to calculate this value. First, I estimated prey abundance within broad habitat types that could be used by the owl and its potential prey. Second, I estimated amounts of these habitats used by the owls when foraging during their breeding season. Lastly, I combined the estimates of prey abundance and foraging habitat used by spotted owls to determine total amounts of prey in the owls' foraging areas. Additional details on sampling and estimating prey abundance, on estimating habitats used by spotted owls, and estimating associated sampling variances are described below.

Prey abundance: I replicated sampling of small mammal abundance at sites within three general habitats (Fig. 3.1.). However, I did not replicate all sites within each

habitat every year, primarily because funding diminished during the study. Within each year, sampling was conducted during early July through mid-August. This period provided the best opportunity for marking enough individuals to use reliable estimators of abundance and represented a time of maximum prey abundance within the period that young spotted owls were being fed. Although small mammal populations are customarily sampled monthly or bi-annually, this single sampling period provided the best benchmark for annual population trends given the study objectives, funding limits, and inclement conditions imposed by the study area. Other investigators have referenced the average number captured between spring and fall trapping sessions to examine owl responses to small mammal populations (Lundberg 1981, Rohner et al. 1995). By using summer values, I approximated the mid-point between minimum numbers of rodents encountered during spring and maximum numbers during early fall.

Additional details on selecting sites for sampling and estimating abundance of small mammals are given in Chapter 2. All trapping and handling procedures followed those recently advocated for proper animal care and use (approved Animal Care and Use Protocol # 92-127A-02, Colorado State University, National Academy of Sciences 1996, American Society of Mammalogists 1998).

Spotted owl foraging areas: I estimated the amount of three habitats (MF-M, MM, and XF) available to Mexican spotted owls for foraging during the breeding season as the amount of area (ha) of each habitat occurring within a 467-ha circle circumscribed around a male owl's center of activity. The size of circle equaled the average size of a male spotted owl's home range (minimum convex polygon method) in the study area estimated from a sample of radio-marked individuals followed during the 1992 or 1993

breeding season (Ganey et al. *in review*; Appendix 3.B). I considered circular areas representative of foraging areas because they comprised similar amounts of habitat compared to two common home-range configurations (minimum convex polygon and 95%-adaptive kernel) estimated from nighttime observations of these radio-marked individuals (Appendix 3.B). I then estimated amounts of habitat in circular foraging areas for all male owls and years from which dietary samples or reproductive data were collected using a geographic information system (GIS; see below). I restricted the area examined to that potentially used by males rather than by pairs because (1) male spotted owls provision both the female and young during most of the breeding season (Gutiérrez et al. 1995), (2) the male and female home ranges tend to greatly overlap during this time (Ganey and Dick 1995), and (3) data on individual females were limited.

During the breeding season, male spotted owls are central-place foragers, generally departing from and returning to the same nesting or roosting area (Carey and Peeler 1995). I therefore used, in order of preference, either the location of a nest, geometric mean of multiple breeding-season roosts, or a single breeding-season roost recorded during spotted owl surveys to represent the center of each owl families' activity. Spotted owl locations were year specific. Consequently, owl-prey habitat values were allowed to vary according to annual shifts in nest- or roost-site selection by these owls, which occurred frequently in this population (Ward and Salas 2000).

I estimated habitat amounts using digital maps of land-management cover types in a geographic information system (ARC/INFO 7.2.1; ArcView 3.0; ESRI 1992). I reclassified land-management cover types originally classified according to vegetative type and general tree-size distributions on lands administered by the Sacramento Ranger

District (USDA Forest Service, Lincoln National Forest, *unpublished data*). The original cover-types were assigned to polygons ($\bar{x} \pm SD$ of area = 23 ± 71.4 ha) based on interpretation of aerial photos (approximately 1:24,000 scale). Non-Forest Service lands were not previously classified. To create a digitized map of spotted owl-prey habitat, I reduced the original classes so that mesic forest included all mixed-conifer (MC) polygons, xeric forest included all ponderosa pine (PP) and pinyon-juniper (PJ) polygons, and montane meadows included all montane grassland (MG) polygons. I created a forth category, other (OT), that included remaining polygons classified as aspen (AS), oak (OK) montane shrubland (MS), desert shrubland (DS), desert grassland (DG), or rock and barren soil (BR). To determine the amount of these four classes occurring on non-Forest Service land, I interactively delineated and recorded sizes of unclassified areas found within owl foraging areas while referencing digital ortho-photo maps (original scale 1:80,000), topography generated from digital elevation models (12.2-m [40-ft] contour interval), and owl-prey habitat occurring on Forest Service lands. Concurrently, I corrected any misclassified Forest Service lands emanating from the original cover type map by referencing the intersection of owl-prey habitat and digital ortho-photo maps. On average, 84 ha of 418 ha (20.1 %) of Forest Service lands originally classified as owl-prey habitat from cover-type maps within the owl foraging areas had to be corrected. The predominant error stemmed from extending forest-type boundaries into meadows. Hence, the meadow habitat type was underestimated by the map of land-management cover types.

Weather. I included two weather factors, cumulative precipitation (cm) and mean minimum temperature (°C) during specific periods, when modeling environmental

influences other than prey amounts on spotted owl reproduction (see below). Site-specific weather values were estimated from linear functions developed between local weather data and elevation. Predictive equations and associated measures of reliability are given in Appendix 3.C.

Data Analysis

Spotted owl diet. I quantified food habits of Mexican spotted owls using two standard measures, relative frequency (%) and percent biomass comprised by prey taxa (Marti 1987). Frequency is useful for relating owl requirements according to prey numbers while biomass conveys energetic value.

I estimated the number of individual prey consumed by recording maximum number of individuals of a given taxa represented by skulls and skeletal remains in spotted owl pellets. For example, if pellet remains included 4 right femurs and 3 left femurs of deer mice, I deduced that four deer mice were consumed. I identified skulls and appendicular skeletal parts using published keys, species descriptions, and a reference collection comprised of small mammals occurring in the Sacramento Mountains (DeRosier and Ward, *unpublished report*). Questionable items were reviewed in conjunction with collections and expertise at New Mexico State University or University of New Mexico. Arthropod (primarily insect) numbers were less precise and often represented presence of parts. I classified items to the most precise taxon possible. Accordingly, I chose to analyze and describe the owls' diet according to 12 prey groups that included all items while minimizing identification bias. These categories were chiefly comparable to the 11 prey taxa presented by Ward and Block (1995). In the latter study, sciurids were included as other medium-sized mammals and soricids were included

as other small mammals. Here, I considered soricids and sciurids as independent groups and I excluded reptiles from consideration because none were recorded.

Relative frequency (p) of each prey group (i) was estimated according to a given owl territory (j) in a given breeding season (k) as:

$$\hat{p}_{ijk} = (f_{ijk} / \sum_{i=1}^{m} f_{ijk}) \cdot 100\% \quad (3.1)$$

where m is the number of prey groups and the summation of f_i equals the total number of prey items (n_j) recovered in an owl territory. I estimated percent biomass (pb_{ijk}) from estimates of biomass (b_{ijk}; in grams) in each prey group as:

$$\hat{pb}_{ijk} = (b_{ijk} / \sum_{i=1}^{m} b_{ijk}) \cdot 100\% \quad (3.2).$$

Biomass was estimated as the product of average mass (g) and frequency of each species represented by a particular prey group. For broader taxa, I calculated a weighted mean mass based on proportion of items found on average in the owl's diet that could be identified to species during a specific year. For example, I estimated biomass of voles (*Microtus* spp.) occurring in the diet of a given spotted owl family as:

$$\hat{b}_{Microtus\ spp.} = (f_{MILO} \cdot \bar{mass}_{MILO}) + (f_{MIME} \cdot \bar{mass}_{MIME}) + (f_{MISP} \cdot [\sum (\bar{p}_i \cdot \bar{mass}_i)/s]) \quad (3.3)$$

where f_{MILO} and f_{MIME} are frequency of long-tailed (*M. longicaudus*) and Mexican voles (*M. mexicanus*) found in the diet of owls from a specific territory, f_{MISP} is the frequency of items classified only as *Microtus* spp., $\bar{p}_i$ is the proportion of species i of a particular

dietary group averaged among data from all owl territories (in this case, *M. longicaudus* and *M. mexicanus*), and *s* is the total number of species of a particular dietary group found in the remains collected from all owl territories in a given year (in this case $s = 2$). I estimated mean mass for frequently trapped species from small mammal capture data. These estimates were year-specific averages from all habitats. I estimated mass for other species from specimens housed in either the Vertebrate Museum of New Mexico State University or the Museum of Southwestern Biology, University of New Mexico. When estimating averages from museum specimens, I chose those individuals most proximal to the study area. For a few of the larger mammals potentially consumed by spotted owls (e.g., some sciurids and *Sylvilagus* spp.), I used the median between 300 g and a minimum based on approximate weight of weaned young (~50 g). I considered the former to be the maximum size prey consumed by Mexican spotted owls. I consulted mass values given by Steenhof (1983) and Dunning (1993) for avian species and then assigned approximate mass values according to the general size of remains (small = 28 g, medium = 75 g, and large = 120 g). For mass of identified owls I referenced Johnsgard (1988). I assigned a mass of 1 g to all arthropod frequencies arbitrarily because species identity was lacking and sizes were difficult to distinguish from the remains. I restricted all analyses of food habits to samples from owl territories that were ≥ 10 items because changes in proportions with total number of items stabilized at this value for most of the common prey groups.

Under this observational study design, little could be said about prey selection, switching, and functional or numerical responses if prey consumption, owl reproductive output, or prey availability remained static over time. I therefore quantified the amount of

temporal variation in dietary and reproductive measures using formulae in Burnham et al. (1987:263). I estimated the average sampling variance of these measures as the mean variation in diet among owl families or reproductive output among owl pairs within each year. These values were subtracted from total variation of six-year means. I expressed the temporal process variation in the owl's diet or reproductive output as a coefficient of variation (CV_Y in %) for each prey taxa and tested its significance following Burnham et al. (1987). Significant temporal variation in the abundance of the owl's common prey was quantified in Chapter 2.

Prey availability. I estimated the total amount (number or biomass) of common prey available in each male owl's foraging range using the following steps. First, I estimated mean density ($\hat{N}$/ha) or biomass (g/ha) of each common prey species occurring in each of the three habitats following procedures described in Chapter 2. Second, for comparison with dietary measures, I summed the density or biomass estimates of respective species to estimate habitat-specific amounts of common prey genera. Third, I estimated habitat-specific numbers or biomass of each common prey taxon (genus level for analyzing dietary responses; species level for analyzing reproductive responses) by multiplying habitat-specific abundance estimates by the hectares of each respective habitat found in each male owl's foraging range. Last, I summed the habitat-specific numbers or biomass of each prey taxa across habitats occurring within each owl foraging range (Appendix 3.B). Sampling variances associated with estimates produced during each step were calculated using the delta method (Bajpai et al. 1978). Because small mammal abundance in meadows was not sampled in 1991, I substituted a 5-yr mean and

associated sampling variance estimated from data gathered in meadows during 1992–1996.

Prey selection. I tested for selection of common prey genera by Mexican spotted owls using two methods. First, I tested for disproportionate use of any of the common prey in each year using a maximum likelihood test (Manly et al. 1993:50):

$$\chi_L^2 = 2\sum_{i=1}^{I=3} [u_i \ln\{u_i / E(u_i)\} + m_i \ln\{m_i / E(m_i)\}] \quad (3.4)$$

where u_i is the frequency of prey i consumed by all spotted owls sampled in a given breeding season, m_i is the number of prey i available to those owls, and the respective expected values are

$$E(u_i) = (m_i + u_i)\, u_+ / (m_+ + u_+) \quad (3.5)$$

and

$$E(m_i) = (m_i + u_i)\, m_+ / (m_+ + u_+) \quad (3.6)$$

with '+' subscripts indicating summations over all prey groups. I pooled data from all owls within a year because expected values of some prey groups in the diet of some owls were <5 and this would have produced unreliable inferences (Manly et al. 1993). I considered the pooled dietary frequencies representative of this spotted owl population during a given year because sampling-among owl variation was low (CV_S <22%). I therefore followed Manly et al.'s (1993) Design I/Sampling Protocol A for quantifying prey selection.

Second, I determined which prey were taken disproportionately by quantifying ratios of relative consumption of each prey to its relative availability (Manly et al. 1993). I estimated these selection ratios (w_i) for each prey group (i) as

$$\hat{w}_i = o_i / \hat{\pi}_i \quad (3.7)$$

where o_i is the proportion of prey in category i consumed by all sampled owls (i.e., u_i / u_+) and $\hat{\pi}_i$ is the proportion of prey i available to those owls (i.e., m_i / m_+; Manly et al. 1993:50). Resource selection ratios found to be significantly >1 would indicate relative selection, ratios significantly <1 would indicate relative avoidance, and ratios equal to 1 would indicate that prey were taken in accordance to their availability. I used Bonferroni confidence limits, adjusted for multiple, simultaneous comparisons, to determine which $\hat{w}_i$ were significant. I estimated the adjusted 95% confidence limits as

$$\hat{w}_i \pm z_{\alpha/2I} \, SE[\hat{w}_i] \tag{3.8}$$

where i is the number of prey groups compared simultaneously. It is important to note that the estimator of sampling variance of $\hat{w}_i$ must incorporate the sampling variation associated with estimating the amount of available prey (Manly et al. 1993). I estimated the sampling variance of $\hat{w}_i$ as

$$\hat{var}[\hat{w}_i] = \hat{w}_i^2[(1 - o_i)/(o_i u_+) + var[\hat{\pi}_i]/\hat{\pi}_i^2] \tag{3.9}$$

where sampling variance of the amount of available prey i was estimated as

$$\hat{var}[\hat{\pi}_i] = \hat{\pi}_i^2[(SD[m_i]/\bar{m}_i)^2 + (SD[m_+]/\bar{m}_+)^2 - (2r_{m_i m_+} \cdot SD[m_i] \cdot SD[m_+])/(m_i m_+)] / n \tag{3.10}.$$

In equation 3.10, $r_{m_i m_+}$ is the correlation between m_i and m_+ and n is the number of owl foraging ranges for which the amount of available prey was estimated. Use of Bonferroni adjusted confidence limits favors reduction of Type I errors over reduction of Type II errors (K. P. Burnham, *personal communication*). Thus, the fact that power to reject a food item as selected could be weak must be considered when drawing inferences. Examination of average trends in prey use versus prey availability over multiple breeding seasons provided addition means for assessing prey selection (see next section).

Functional response. The above procedures allowed me to test for significant selection of a given prey group during a given year. To summarize a relative functional response of Mexican spotted owls to their common prey over all six breeding periods, I regressed the proportion of each prey consumed against the proportion available to the owl population in every year of the study (Murdoch and Oaten 1975, Rohner et al. 1995). I first transformed these data using an arcsine-square root function to approach normality (Zar 1984:240). I then tested each regression slope against a null value of 1.0. Slopes significantly >1 would indicate disproportionately positive response to that prey, on average, during the period of study. I used this same approach to quantify the owl's relative response to biomass of each common prey genera. The latter would indicate if Mexican spotted owls were responding to prey size in addition to prey numbers.

I quantified the owl's absolute functional response by plotting the average number of each common prey genera consumed during the breeding season as a function of the prey's available numbers (i.e., number in a 467-ha foraging area). Because dietary frequencies were based on samples useful for estimating proportions but not absolute numbers of prey consumed, I estimated the latter as a product of respective dietary proportions and the amount of prey required to meet energetic needs during the breeding period (Lundberg 1981, Lindén and Wikman 1983, Korpimäki and Norrdahl 1991, Nielsen 1999). For the latter, I modified a model used previously to estimate energetic requirements of northern spotted owls (Ward et al. 1998; Appendix 3.D). I used linear and nonlinear regression to evaluate fit of absolute functional responses to each common prey to three general types of functions (number consumed [N_c] | number available [N_a]) predicted by Holling (1959). These included a (1) line with positive slope (N_c =

a + b·N_a), (2) negative hyperbola ($N_c = N_a$ / a·N_a − b), and (3) sigmoidal curve (N_c = 1/[a + be^{-Na}]). Barring reasonable fit to these general forms, shape of the functional response was evaluated against other possible forms (Daniel and Wood 1980, Fujii et al. 1986). Being limited to six breeding seasons, I considered the analysis of response form more descriptive than inferential (Trexler et al. 1988).

Prey switching. If Mexican spotted owls switch to alternative prey, then selection of these prey should increase as primary prey diminish in availability (Murdoch 1969). Thus, to test for switching behavior I quantified the correlation between prey selection ratios (w_i) and availability of the prey that was most consistently selected by the owls (Korpimäki 1992). I examined w_i for this test because these measures also accounted for changes in the diet due to changes in the prey's own abundance. Significant negative correlations $r < -0.70$; $\alpha = 0.05$) would indicate prey switching. Because evidence for switching may be conveyed by disproportionate relationships and hence curvilinear functions (Murdoch and Oaten 1975, Real 1989), I also examined the graphical relationship between w_i of common alternative prey and available amounts of primary prey.

Prey preference. According to theory and experimental work, a predator will take preferred prey in disproportionately greater amounts when satiation is approached (Murdoch and Oaten 1975, Ellis et al. 1976). I tested this idea by examining prey selection as a function of food surplus. I used $\hat{w}_i$ as a measure of selection and I estimated the food surplus as a ratio between total common prey biomass (kg) available and total biomass required to meet the owl's energetic demands during the breeding season (Appendix 3.D). Here, I assumed that Mexican spotted owls approached satiation

as food surpluses increased. Accordingly, selectivity of preferred prey should be positively correlated with the potential for satiation.

Reproductive Response. I quantified reproductive output of Mexican spotted owls ($\hat{RO}_{it}$) as the number of young observed outside of a nest (≈ fledged) for each adequately surveyed pair (at territory *i*) in a given year (*t*). I examined reproductive responses at two biological levels, one that focused on owl reproductive potential within a particular territory, and the other that focused on average reproductive output by the population. To quantify reproductive potential ($\hat{RP}_i$), I divided the total number of young found at a given territory *i* during years that the territory was adequately surveyed by the maximum number of young that could have been produced in that territory ($Rmax_i$). A pair of spotted owls usually produces no more than three young in a given year (Gutiérrez et al. 1995, LaHaye 1997). Thus, $Rmax_i$ was calculated as number of years a territory was adequately surveyed multiplied by three young per year. I examined reproductive potential instead of total number of young found because independent territories were not surveyed equally among years. Annual reproductive output in the population ($\bar{RO}_t$) was estimated as the average number of young found across all adequately checked pairs in a given year. Female fecundity would equal one-half of this value when sex ratio of fledglings was 50:50 and no unmated females occurred in the territorial population. Scrutiny of the survey protocol and data indicated that subadult individuals were not always distinguished from adults. Thus, reproductive output could not be partitioned among different age classes within the study population.

I evaluated reproductive responses by Mexican spotted owls to availability of each common prey species and several other sources of environmental variation (e.g., amount

of different foraging habitats; weather variables) in two ways. First, I formulated several competing models that hypothesized the effects of environmental factors on the owl's reproductive potential. Then, using an information-theoretic approach to model selection, I identified the most likely factors. This approach was similar to that used to identify factors affecting abundance of the owl's common prey (see Chapter 2) and has been used to quantify factors that likely affect fitness of northern spotted owls (Franklin et al. 2000). Second, I quantified correlations and produced bivariate plots between annual reproductive output and factors describing availability of prey, weather, and amount of habitat. Relationships between prey availability and annual reproductive output were used to describe the short-term numerical response, whereas results from the models and correlation analyses were used to describe the relative influence of multiple environmental factors on the owl's reproductive output. Additional details on these analyses are given below.

Model development: I developed a series of *a priori* models describing potential effects of environmental factors on reproductive potential of Mexican spotted owls from relationships either quantified or proposed in the literature. General factors that might limit spotted owl reproduction include food supply, competition, predation, weather, genotype, individual behavior, and habitat condition (see discussions by Franklin et al. 2000, and North et al. 2000). Models developed and analyzed in this study focused on three of these factors, food supply, weather, and habitat condition.

Food supply is usually perceived to have a direct and positive influence on spotted owl reproduction. To date, no studies have demonstrated a correlation or experimental link between the owl's reproductive output (number of young produced) and prey

abundance, availability, or consumption. The relationship is frequently presumed from research showing that successfully breeding pairs (i.e., those that produce at least 1 fledgling) of northern and California spotted owls have greater proportions of larger prey (predominately woodrats) in their diet (Barrows 1987, Thrailkill and Bias 1989, White 1996, Smith et al. 1999). Evidence also stems from foraging patterns and habitat use that coincide with greater use of larger prey, which likely provide an energetic benefit (Carey et al. 1992, Carey and Peeler 1995, Zabel et al. 1995, Ward et al. 1998). In contrast, reproductive success by Mexican spotted owls has not been related to consumption of larger prey (Ward and Block 1995, Seamans and Gutiérrez 1999). Rather, prey diversity and total prey biomass are presumed to influence reproduction in the Mexican subspecies, particularly in southern portions of its range (Ward and Block 1995).

Weather may exert a direct or indirect influence on reproduction by spotted owls. Number of young per pair or female fecundity of northern spotted owls has been negatively correlated with number of days of precipitation during the late nesting season (May; Franklin et al. 2000), total precipitation during the entire nesting period (March–June; Zabel et al. 1996), or total precipitation during a prolonged period preceding raising of young (e.g., September–April; Wagner et al. 1996). Similarly, reproductive output by California spotted owls was found to be greater when < 21 cm of precipitation fell during March–May and, if occupying conifer forest at higher elevations, when minimum temperature during April exceeded −2° C (North et al. 2000). Although the precise mechanisms underlying these relationships were unknown, rainfall during the nesting season may have reduced ability of male owls to procure food for nesting mates or hatchlings and possibly increased energetic demand (Zabel et al. 1996, Franklin et al.

2000). For the prolonged period (over winter and during early nesting periods), less precipitation may have been associated with prevalence of high-pressure weather systems and hence milder winter conditions that permitted more energy to be allocated toward reproduction the following spring (Wagner et al. 1996). Lower April temperatures may also have increased energetic demand. Indirectly, temperature and precipitation may have influenced the owl's reproductive output through effects on prey abundance. Excessive wet or dry periods may reduce abundance of some of the owl's prey species (Franklin et al. 2000).

Habitat condition and distribution may influence reproduction in a spotted owl population in several ways. First, nesting sites, defined by forest structures related to tree size (or age), late stages of decay, or by platforms created by other raptors or tree pathogens (Gutiérrez et al. 1995), could be limited on the landscape. Second, prey abundance or accessibility could be limited by habitat structure or composition. Third, suitable cover from predation or weather could be lacking or limited. Finally, the distribution of suitable habitat patches may be dispersed enough to prohibit successful location of a mate.

Partitioning of these specific effects on spotted owl reproduction has rarely been attempted. Instead, the influence of habitat condition on the owl's reproduction has been approached by searching for associations with amounts of a particular vegetation community or successional stage that includes a combination of the properties required for successful reproduction. For example, specific measurements taken at nest sties of California spotted owls were not found to be associated with reproductive success (production of at least one fledgling) whereas productivity (number of fledglings per

successful nest) was found to be greater for owls occupying oak/big-cone fir (*Quercus chrysolepis*/*Psuedotsuga macrocarpa*) forest or oak woodlands when compared to owls occupying mixed conifer forests of higher elevation (LaHaye et al. 1997, North et al. 2000).

Associations between vegetation type or seral stage and reproduction by northern spotted owls have also been reported but the specific predictor variables have varied by geographic region and scale of analysis. For example, in analysis of a single year of survey data that spanned the subspecies range, Bart and Forsman (1992) found that amount of late-seral (>100 yr) conifer forest in ~20-km^2 compartments was positively correlated with the number of owls fledged per pair. In contrast, Meyer et al. (1998) found very few correlations between the owl's reproductive output over multiple years in Oregon and predictors describing habitat condition within circles ranging 2–36 km^2 in size and centered on nest locations. For a spotted owl population in the Klamath Mountains, Meyer et al. (1998) reported that fractal dimension of the forested landscape within and surrounding owl roosts, number of late-seral, mixed conifer patches, and amount of hardwood forest type were positively associated with reproductive output (averaged over time). For another population of northern spotted owls occurring in the Klamath Mountains of northern California, Franklin et al. (2000) found that the owl's reproductive output in a territory was greatest when the nesting and roosting area was comprised by one relatively small core patch of late-seral, mixed evergreen forest with a great amount of edge. This combination of features presumably provided the environment required for nesting and roosting while offering greater access to a key prey species (dusky-footed woodrats; Ward et al. 1998, Franklin et al. 2000). Finally, in a

managed landscape in the coastal mountains of northern California, Thome et al. (1999) found that higher reproductive success (proportion of years where ≥1 fledgling produced) was associated with greater amounts of forest with tree basal area ranging 23–45 m^2/ha, greater amounts of forest with trees ranging 61–80 yrs in age, and lesser number of residual trees/ha. Thome et al. (1999) suggested that their results were likely explained by the distribution of the owl's predominant prey; dusky-footed woodrats.

From these relationships, I developed one global model (Global) and 23 candidate models (C1–C23) for assessing which factors were most likely to influence the owl's reproductive potential (Table 3.2). I limited the global model of reproductive potential to seven ecological regressors. This resulted in a minimum 66:9 ratio of sample size (number of owl territories where number of fledglings was recorded in ≥1 yr) to estimated parameters (K = seven coefficients of ecological regressors, an intercept coefficient, and estimate of regression variance term). This series of models allowed me to distinguish among influences related to availability of common prey species, weather, and amount of habitat.

In the global model, I assumed that colder temperatures during late fall–winter (November–February; FWTEMP) increased energetic demand, and hence were positively associated with lower production of young. This particular variable was not cited in the literature on spotted owls. However, I considered it a useful index of energy demand and, hence, female condition prior to the onset of breeding in a given year. Body condition during winter has been known to affect follicle development in female tawny owls in the subsequent spring (Hirons 1982). In addition, I assumed that total precipitation during the nesting period (March–May; NSTRAIN) would have a negative impact on spotted

owl reproduction, and that total biomass (kg) of each of the owl's five most common prey species was positively associated with production of its young (Table 3.2).

Each of the *a priori* candidate models was either a logical subset of the global model or included substitute parameters (Table 3.2). For example, in models C5 and C21 total biomass of the five common prey species within the mesic forest habitat (MFPREY) was used as a measure of prey availability, rather than the availability of a given species in all three habitats. A stronger association between owl reproduction and amount of common prey in mesic forest would be expected over other measures of prey availability if mixed-conifer forest was the owl's most important foraging habitat. However, if total biomass of multiple prey species from multiple habitats was important, then all five species of common prey occurring in mesic forest, meadows, and xeric forest (COMPA) or biomass of mice and voles in all three habitats (SMLPA) would be expected to have a stronger association with reproduction (see models C10–C13, C15, C16, C19, C20 in Table 3.2). If the amount (ha) of mesic forest (MFHA) or if habitat diversity (evenness index; HABEV) could provide a surrogate measure of prey availability, then models C6, C14, C17, C18, C22, or C23 would be expected to provide a stronger association with the owl's reproductive potential (Table 3.2). Habitat evenness was calculated following Meyer et al. (1998:14; see also Pielou [1969]) as,

$$HABEV = -(\sum_{i=1}^{s=4} p_i \ell n p_i) \; / \; \ell n(s) \qquad (3.11)$$

where p_i is the proportion of each of four (s) habitat types .

In model C8, I substituted total precipitation (cm) during fall through to the spring (September–April) preceding a given breeding period (PFSRAIN) for NSTRAIN. PFSRAIN might have a negative effect on the owl's reproductive potential (as observed

by Wagner et al. 1996) or a positive influence if rainfall is not excessive and improves conditions for the owl's prey. In model C8, PSFRAIN was assumed to have a negative influence on reproductive potential (Table 3.2). Further, in model C9, I substituted minimum temperature during the early nesting period (April; ENTEMP) for FWTEMP. If cold temperature during the early nesting cycle was more critical to reproductive output than the effects of cold temperature over winter, then model C9 would show a stronger association than model C7.

Following analysis and review of all *a priori* models, I developed and estimated parameters for eight exploratory models (Table 3.2). The general purpose of the exploratory models was to develop a most parsimonious model of factors influencing the owl's reproductive potential. Models E1–E3 and E7 included primarily reduced combinations of the most likely factors identified during analysis of the *a priori* models. Models E4–E6 included the same factors as models E1–E3, respectively, except that values of the regressor variables (SNSTRAIN, SSMLPA, SCOMPA, SMFPREY) were estimated as cumulative sums, rather than mean values across years in each owl territory. These latter models were used to assess whether data type (means or sums) influenced model performance. Cumulative sums may have represented energetic costs or supplies more accurately than average values which would smooth out high and low values. In model E8, I examined the relationship between elevation and reproductive potential. I assumed a quadratic structure for this model based on inspection of a bivariate plot of elevation and the owl's reproductive potential. Using this form of structure would imply that there is a mid-range of elevation (ELEV) at which reproduction is maximized (Table 3.2).

Model parameter estimation: I formalized each set of hypothesized effects on owl reproduction as a linear regression model. The general form used to model reproductive potential of Mexican spotted owls was:

$$\hat{RP} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 \ldots \beta_p X_p + \in \quad (3.12).$$

The number of independent environmental variables (p) varied with each model, as described above (Table 3.2). Here, $\in$ signifies the residual error, or amount of variation in owl reproductive potential not explained by the hypothesized effects. I used the method of least squares to estimate model coefficients (β_j). I transformed reproductive potential using an arcsine-square root function prior to parameter estimation (Zar 1984). I treated the assumptions associated with this type of model as in Chapter 2.

The observations for each regressor variable (X_i) were territory-specific. In most cases, each observation was an average value for the time-period corresponding to when the number of young were recorded in each territory. For example, if a particular territory was adequately surveyed in 1992 and 1995, then FWTEMP for this territory would be calculated as the mean minimum temperature during November 1991 through February 1992 and during November 1994 through February 1995. This procedure was necessary to match multiple seasons of environmental data with the corresponding measure of spotted owl reproduction. The exception was for models E4–E6 where the regressor variables were represented by cumulative sums over a specific time period.

Model selection: I used Akaike's corrected criterion (AIC_c) as a means for selecting among models. Specifically, I used AIC_c to rank each model and to calculate a weight for gauging relative importance of factors affecting the owl's reproductive potential and estimating unconditional variances of effect coefficients. I calculated AIC_c

with output from regression results following Burnham and Anderson (1998:48), as:

$$AIC_c = n \cdot \ell n(\hat{\sigma}^2) + 2K + \frac{2K(K+1)}{(n-K-1)} \quad (3.13).$$

Here, $\hat{\sigma}^2$ is the residual sums of squares divided by n, and K is the number of estimated parameters including an intercept and $\hat{\sigma}^2$. I reported the change in AIC_c ($\Delta AIC_c = AIC_c - \min AIC_c$) for each model as a relative measure of difference among models. I calculated an Akaike weight (Aw_j) for each model j following Burnham and Anderson (1998:124) as:

$$Aw_j = \frac{\exp(-\frac{1}{2}\Delta_j)}{\sum_{r=1}^{R} \exp(-\frac{1}{2}\Delta_r)} \quad (3.14),$$

where R is the total number of models examined, Δ is the abbreviated symbol for change in AIC_c for a given model. These weights portray the probability that a particular model is "best" given the set of models examined and data collected. I reported a 95% confidence set as those models ranked according to ascending ΔAIC_c with a sum of $Aw_j \geq 0.95$. The best model would be expected within this confidence set 95% of the time.

In multiple regression, estimates of model coefficients can vary according to variation within data observations and the composition of regressors (i.e., structure) in the model. In addition, structure of the "best" model may vary with analysis of different samples of data, a condition referred to as model uncertainty. I incorporated these types of variability in estimating model coefficients by estimating mean coefficients (weighted across models) and unconditional variances associated with the model-averaged parameters (Burnham and Anderson 1998:133–135). The mean coefficient for a given regressor variable ($\bar{\beta}_i$) averaged over all models that included $\hat{\beta}_i$ was estimated as:

$$\bar{\hat{\beta}}_i = \sum_{j=1}^{R} Aw_j \hat{\beta}_{ij} \quad (3.15),$$

with an associated unconditional variance:

$$\hat{var}(\bar{\hat{\beta}}_i) = \left[\sum_{j=1}^{R} Aw_j \sqrt{\hat{var}(\hat{\beta}_{ij} \mid M_j) + (\hat{\beta}_{ij} - \bar{\hat{\beta}}_i)^2} \right]^2 \quad (3.16).$$

In equation 3.16, $\hat{var}(\hat{\beta}_{ij} \mid M_j)$ is the square of the standard error for a particular regressor coefficient estimated for a given model M_j. I expressed unconditional variation as a coefficient of variation of the model-averaged value ($CV\ [\bar{\hat{\beta}}_i]$), estimated as:

$$CV\ [\bar{\hat{\beta}}_i] = \frac{\sqrt{\hat{var}(\bar{\hat{\beta}}_i)}}{\bar{\hat{\beta}}_i} \cdot 100\% \quad (3.17).$$

Relative importance (RI) of each regressor was quantified as the sum of Akaike's weights across all models that included that regressor. RI could range from 0 to 1.

I used SAS (SAS Institute 1994; 2000) for all computations and statistical analyses. Unless noted otherwise, inferential tests were based on nominal levels of Type I errors $\leq 5\%$.

Correlations with annual reproduction: Following formulation and evaluation of models of the owl's reproductive potential, I quantified Pearson product-moment correlation coefficients for describing relationships between annual mean reproductive output in this spotted owl population and temporal changes in amounts of common prey or weather variables. Although limited to six years of examination, these bivariate relationships reflected covariation through time, rather than spatial variation among owl territories as was analyzed through the modeling approach described above. Strong correlations *(*$r > 0.60$, $P > 0.05$) or notable nonlinear patterns in bivariate plots were offered as evidence of factors that may be affecting annual reproductive output of

Mexican spotted owls in the Sacramento Mountains and that should also be considered in future investigations.

RESULTS

During six breeding seasons (1991–1996), 2,286 prey items were collected and identified from 48 Mexican spotted owl territories. After excluding data from owl territories where <10 prey items were collected, 2,138 prey items from 36 owl territories were analyzed. Dietary samples were not gathered from all territories every year. Diet data were available from 23 of these owl territories (64%) during 1 breeding season only; from four, six, two, and one territory during 2, 3, 4, and 5 breeding seasons, respectively. None of the 36 territories was sampled in all six years. Assuming that each breeding season constituted an independent event, these data comprised dietary samples from 62 owl-family units.

During July through August of the same six years, 142,186 trap-checks within three habitat types (MF-M, MM, XF) resulted in captures of 22 species of mammals, including 3 soricid, 2 leporid, 14 rodent, 2 mephitid and 1 mustelid species (see Chapter 2:Appendix 2.B). The majority (94%) of individuals marked for study was comprised by 5 murid species: deer mouse (*P. maniculatus*), brush mouse (*P. boylii*), Mexican vole, long-tailed vole, and Mexican woodrat (*N. mexicana*) (n = 6,859 individuals). Six-year average mass in grams (± SE; all individuals encountered) for each of these species was, respectively, 17.2 ± 0.09, 23.8 ± 0.23, 28.5 ± 0.19, 33.3 ± 0.36, 118.7 ± 2.55.

Sixty-six unique owl territories were surveyed adequately to determine the number of young present during 1991–1996. Nine of these 66 were surveyed during one breeding season only, 19 during two breeding seasons, 10 during three breeding seasons,

15 during four breeding seasons, 10 during five breeding seasons, and three territories were adequately checked during all six breeding seasons.

Spotted Owl Diet

During the breeding season, Mexican spotted owls occurring in the Sacramento Mountains consumed a variety of prey, including 19 species of mammals and one bird species, two other mammal species identified only to genus, and a number of items identified to broader taxanomic categories (e.g., class, order, or family; Appendix 3.E). Using the mass values given in Appendix 3.F, I estimated that 87.5% of the prey items and 95.8% of the biomass consumed was comprised of small or medium-sized mammals over the 6-year period (Tables 3.3, 3.4). The most common prey by frequency included three genera, *Peromyscus*, *Microtus,* and *Neotoma*, which comprised 67.2% of all items consumed (Table 3.3). These same genera comprised 55.9% of biomass consumed (Table 3.4). I will refer to these three genera respectively as mice, voles, and woodrats. These common prey were comprised primarily of five species: deer mouse, brush mouse, Mexican vole, long-tailed vole, and Mexican woodrat (Appendix 3.E). Of the 503 prey items identified as species of white-footed mice, 68.4% were deer mice, 28.2% were brush mice, and 3.4% were rock mice (*P. nasutus*). Of the 307 prey items identified as species of voles, 66.4% were long-tailed voles and 33.6% were Mexican voles. Of the 158 prey items identified as species of woodrat, 95.6% were Mexican woodrats and 4.4% were white-throated woodrats (*N. albigula*). Only one other prey group, rabbits (*Sylvilagus* spp.), comprised >10% of the biomass in the owl's diet. The amount of rabbit biomass consumed (17.9%), however, was based on a median size of 125 g, which would be an overestimate if the owls preferred young rabbits. Because of the uncertainty in the

size of rabbits consumed and because relatively few were consumed (5.7%), I did not consider them common prey of Mexican spotted owls during the six breeding seasons.

Consumption of common prey varied significantly among breeding seasons (Tables 3.3, 3.4). Of the three common taxa, consumption of woodrats varied the most by frequency and least by biomass (CV_Y = 47.6% and 30.0%, respectively). According to frequency of items, mice were taken most frequently and dominated the diet during breeding seasons of 1991, 1994, 1995, and 1996 (Fig. 3.2a). Voles were taken most frequently in 1992 and 1993 (Fig. 3.2a). Fewer woodrats were consumed relative to other common prey except in 1995 (Fig. 3.2a). However, when biomass was considered (Fig. 3.2b), the relative importance of woodrats in the owl's diet increased and mice appeared less important.

Trends in both dietary measures indicated shifts in consumption of common prey over time but were most apparent in percentage of biomass consumed by owls (Fig. 3.2b). For example, biomasses of mice and woodrats were consumed in relatively greater amounts in 1991. Consumption shifted to voles and woodrats in 1993, and finally to predominately woodrats in 1995 and 1996 (Fig. 3.2b). Consumption of Botta's pocket gopher (*Thymomys bottae*), other medium sized mammals, other small mammals, and arthropods was also significantly variable over time (Tables 3.3, 3.4). However, variation in the other medium and small mammals consumed may have simply reflected variation in the extent of incomplete skeletal material found in the diet because these categories included material that could not be classified beyond the "class" level. In contrast, the amount of soricids, chiropterans, leporids, sciriuds, and avian species consumed appeared consistently low among owls and years (Tables 3.3, 3.4). Thus, consumption of two

uncommon prey, pocket gophers and arthropods, also varied significantly through time.

Variation in amounts of most prey species consumed among owl territories was generally less than annual variation. CV_S for percent biomass of the three common prey groups (mice, voles, and woodrats) ranged from 14% to 23% (Table 3.4). Low variation among diets of owls in different territories may be indicative of similarity in quality of foraging habitat or low plasticity in foraging habits among individuals occupying those territories.

Prey Availability

The amount of each common prey available to Mexican spotted owls during the six breeding seasons was similarly dynamic (Fig. 3.2c and d). Mice were most abundant in 1991 ($\bar{x}$ = 17,447 mice or 282 kg/owl foraging range), primarily as a result of irruption of deer mice in mid-seral mesic forests (Fig. 3.2c and d; Chapter 2:Fig. 2.4). The amount of mice available to owls declined greatly in 1992, remained low in 1993, and was at its lowest in 1995 ($\bar{x}$ = 2,121 mice or 40 kg/owl foraging range). Moderate amounts of mice were available to owls in 1994 and 1996 (Fig. 3.2c and d). Voles were most abundant in 1992 ($\bar{x}$ = 8,919 voles or 288 kg/owl foraging range), primarily because both vole species were abundant in meadows and long-tailed voles were concurrently abundant in mesic forests (Fig. 3.2c and d; Chapter 2:Fig. 2.4). The amount of voles available to spotted owls decreased to a low in 1994 ($\bar{x}$ = 637 voles or 20 kg/owl foraging range) then increased to moderate amounts in 1996 (Fig. 3.2c and d). The amount of woodrats available to owls, predominately Mexican woodrats from mesic and xeric forests (Chapter 2:Fig. 2.4), was relatively limited and less dynamic over the six breeding seasons, ranging from a low in 1991 ($\bar{x}$ = 217 woodrats or 25 kg/owl foraging range) to a

high in 1992 ($\bar{x}$ = 533 woodrats or 65 kg/owl foraging range; Fig 3.2c and d).

In general, availability of mice was most variable over time (CV_Y of available biomass = 86%), followed by that of voles (CV_Y of available biomass = 80%), whereas availability of woodrats was the least variable (CV_Y of biomass = 34%). Amounts of deer mice and woodrats in spotted owl foraging ranges were negatively correlated (Pearson correlations for number $r = -0.68$, $P < 0.001$; biomass $r = -0.66$, $P < 0.001$, $n = 62$), indicating that trends in availability of these two prey were asynchronous. The amount of voles and woodrats available to spotted owls was not significantly correlated (number $r = -0.15$, $P = 0.253$; biomass $r = -0.04$, $P = 0.730$, $n = 62$). In contrast, amounts of mice and voles in spotted owl foraging ranges were positively correlated (number $r = 0.59$, $P < 0.001$; biomass $r = 0.54$, $P < 0.001$, $n = 62$), indicating synchronous trends in their availability.

Prey Selection

Log-likelihood χ^2 tests of numbers of common prey consumed and available indicated that some form of disproportionate use of prey by Mexican spotted owls occurred during each of the six breeding seasons (Table 3.5). Selection or avoidance of common prey was most likely in 1991 and least likely in 1995.

Confidence intervals around selection ratios indicated that mice and voles were avoided or taken in accordance with their availability in most years (Table 3.5). Exceptions to this pattern were observed in 1992, when owls took proportionately more mice, and in 1993 and 1994, when owls took proportionately more voles. In contrast, Mexican spotted owls took proportionately more woodrats in each of the six breeding seasons when the numbers available were analyzed or in five of six breeding seasons

when available biomass was analyzed (Table 3.5). Mice and voles were selected when their availability was lowest, whereas woodrats were selected irrespective of their availability (Fig. 3.2c and d; Table 3.5).

Functional Response

Regressions of transformed dietary and availability proportions from all six breeding seasons indicated that relative functional responses of Mexican spotted owls to their common prey were essentially linear (Fig. 3.3) . However, regression slopes, which quantified the intensity of response, differed between the smaller and larger prey. Mice and voles were avoided slightly in proportion to their availability giving slopes approximately <1 (mice: 95% CI of slope for frequency data = 0.729–1.070, for biomass data = 0.621–0.914; voles: 95% CI of slope for frequency data = 0.616–1.150, for biomass data = 0.489–1.030). In contrast, woodrats were taken selectively over other common prey species, which produced a steep linear response with slope >1 (95% CI of slope for frequency data = 1.200–2.330; for biomass data = 1.060–2.000).

Absolute functional responses showed greater variability among the three common prey genera (Fig. 3.4). The owl's response to absolute abundance of mice was distinctly linear ($N_c = 0.018 \cdot N_a$), increasing at a constant proportion (Fig. 3.4a). This amounted to a six-fold increase in consumption of mice with an eight-fold increase in mouse numbers. The response to absolute abundance of voles followed a negative hyperbola ($N_c = N_a / 0.012 \cdot N_a - 3.00$), whereby proportionally fewer voles were consumed as their absolute abundance increased to a saturation point, after which consumption became independent of increases in the vole's abundance (Fig. 3.4b). This amounted to a three-fold increase in vole consumption over an 11-fold increase in vole numbers. The

response to woodrats appeared to be parabolic in function ($N_c = 0.201 \cdot N_a - 0.0003 \cdot N_a^2$). In this case, absolute number of woodrats consumed increased disproportionately and then decreased as absolute availability increased. This pattern indicated that more absolute numbers of woodrats were taken at moderate rather than at higher availabilities (Fig. 3.4c). All equations were forced through the origin, (i.e., all intercepts were set to 0) but the intercept was not included in the sample for estimating parameters. All estimated coefficients were significantly different from 0.

Prey Switching

Given a consistent selection by Mexican spotted owls, I considered woodrats as primary prey for examining switching behavior. Selection of mice $r = 0.42$, $P = 0.402$) or voles $r = -0.40$, $P = 0.433$) was not significantly correlated with available biomass (kg) of woodrats. However, selection of voles was significant (95% CI >1) in two of the three summers (1993 and 1994) of lower availability of woodrats but the overall trend was non-linear and partially confounded with selection of mice (Fig. 3.5). For example, in 1991, when available biomass was as low as in 1994, voles were not selected in greater proportion than available. However, deer mice irrupted during this summer and were taken in great amounts in proportion to their availability (Figs. 3.2d, 3.4). These patterns offered some evidence that these spotted owls switched to alternative prey when woodrat availability was low and indicated that prey switching involving multiple species may lead to complex patterns that cannot be detected by simple correlation analyses.

Prey Preference

Selection of woodrats by spotted owls was positively correlated *(*$r = 0.80$, $P = 0.054$) with food surpluses, indicating that this prey was preferred. Mice *(*$r = 0.67$, $P =$

0.143) and voles ($r = -0.59$, $P = 0.214$) were not significantly correlated with potential satiation. However, the trends depicting woodrat and vole selection were non-linear (Fig. 3.6). The negative trend in vole selection was in sharp contrast to that for woodrats. Selection of voles was significant when food surpluses (and potential satiation) were lowest but diminished rapidly with increases in food supply. Selection of mice was linear showing a gradual increase with satiation but this trend was not statistically significant (i.e., slope $\neq 0$).

Owl Reproductive Potential

Twenty-four original and eight exploratory models were developed and parameterized to distinguish factors that likely influenced reproductive potential of Mexican spotted owls. The number of parameters estimated for each of these models ranged from three to nine (Table 3.6). Fit of the global model (RP_{Global} of Table 3.2), as judged by the amount of variation in the owl's reproductive potential explained by modeled effects (R^2), was low (23.2%). Thus, none of the factors modeled here appeared to exert a strong or dominant influence on this owl's reproductive potential.

Four models appeared to violate the assumption of homoscedasticity (C1, E4, E5, and E6; P of $\chi^2 < 0.05$). However, none of these models was weighted heavily in the ranking procedure. In one of the 32 models (C4), one standardized residual exceeded the range −3.0 to 3.0. Plots of standardized residuals from all models showed random patterns. Overall, then, the models appeared to satisfy the assumptions of multiple linear regression.

Of the 24 original models examined, 12 models comprised a 95% confidence set (Table 3.6). Weights of these 12 models were similar. A most likely model was not

apparent in this set. Model C10 was weighted most heavily (0.1604) but not much greater than models C11 (0.1589) or C21 (0.1194). These top three *a priori* models included a total of five regressor variables (NSTRAIN, ENTEMP SMLPA, COMPA, and MFPREY) whereas 10 regressors were included in the 95% confidence set of original models (Tables 3.6 and 3.7). Only NSTRAIN was ranked relatively high in importance (RI = 0.733). The model-averaged coefficient for this regressor variable was negative, indicating that the influence of rain during the nesting season had a negative influence on the owl's reproduction, as predicted (Table 3.7). The unconditional variance of this coefficient was the lowest among that for all other coefficients (CV = 60%), providing additional evidence that this factor was more likely to exert an influence than the others examined in the original model set (Table 3.7). Although FWTEMP was not included in the top three models, this factor was ranked moderately high (RI = 0.447) in importance. Sign of the associated coefficient, however, was counter to that predicted, indicating that colder fall-winter temperatures were associated with greater reproduction (Table 3.7). Also, variation of the coefficient value was much less consistent (CV = 136.3%) compared to that for other regressors (Table 3.7). Three other factors were ranked as moderately important, ENTEMP, SMLPA, and COMPA (RI = 0.335, 0.331, and 0.322, respectively). The influence of each of these factors matched that predicted (Table 3.7). Consistency of associated coefficients among the original models was moderate (CV = 96.0%, 76.5%, and 77.4% respectively).

Four of the eight exploratory models (E8, E3, E1, and E2) proved slightly more parsimonious than the 24 *a priori* models (Table 3.6). The 95% confidence set of all models (original and exploratory) included these four exploratory models and 11 of the

original candidate models. Akaike weights within this 95% confidence set of models ranged from 0.1196 to 0.0113. Similar to the original model set, the addition of exploratory models did not distinguish a single model as "most likely."

The most heavily weighted model (Akaike weight of 0.1196) in the combined model set predicted the owl's reproductive potential as a quadratic function of elevation. However, the relative importance of elevation compared to other regressor coefficients was low and imprecise (Table 3.7). In general, relative importance of each factor decreased slightly with addition of the exploratory models but the order remained similar with two exceptions (Table 3.7). Relative importance of the availability of mice and voles (SMLPA) and all five common prey species (COMPA) for predicting the owl's reproductive potential was slightly greater than minimum temperature during fall-winter (non-breeding period) or the early nesting period (Table 3.7).

Comparing the Akaike weights among particular model structures identified several patterns. First, models with factors describing habitat condition were poor predictors of the owl's reproductive potential relative to models that included factors describing weather or prey availability (Table 3.6). For example, relative importance of the two habitat regressors (MFHA and HABEV) were low (RI = 0.007 and 0.005, respectively) and were not included in either 95% confidence set of models (Table 3.7). Second, models that included factors describing weather and prey availability had greater weights than those including influences only of weather or only of prey availability (e.g., models C10 and C11 versus models C9 , C19, and C20; Table 3.6). Third, models that included availability of prey aggregated among species were better predictors of the owl's reproductive potential than models that included availability of single prey species. For

example, RI of SMLPA, COMPA, and MFPREY = 0.331, 0.322, and 0.189, whereas RI of PEMAA, PEBOA, MILOA, MIMEA, and NEMEA = 0.117, 0.117, 0.026, 0.026, and 0.008, respectively. Notable was the relative lack of influence that woodrat availability played in predicting the owl's reproductive potential (Table 3.7). Finally, values of key regressors estimated as cumulative sums were poorer predictors than when values were estimated from temporal averages. Relative importance of SNSTRAIN, SCOMPA, SSMLPA, and SMFPREY were < 0.006 (Table 3.7). These variables were not included in any model of the 95% confidence set.

I summarized the influence of the examined factors on the owl's reproductive potential with two models (Fig 3.7). One model included three weather factors, mean minimum temperature during fall–winter (FWTEMP), total precipitation during nesting period (NSTRAIN), and mean minimum temperature during the early nesting period (ENTEMP), and one factor describing prey availability (SMLPA). Availability of mice and voles was used in place of availability of all five common prey in a male owl's foraging range (COMPA) or only within the mesic forest habitat (MFPREY) because the relative importance of SMPLA was slightly greater (Table 3.7). Coefficients averaged across all *a priori* models were used to parameterize this model (Fig. 3.7a). The second model included three of these same variables, excluding ENTEMP and was parameterized using coefficients averaged among all models. ENTEMP was excluded in this summary model (Fig. 3.7b) because its relative importance decreased when all models were considered. However, fit of either model is weak and bivariate plots between the owl's reproductive potential and each variable in the model do not show any obvious relationships (Fig. 3.7). The relationship with elevation, the factor identified by

the top-ranked model was also weak (Fig. 3.7g).

Annual Reproductive Output

Three variables associated with prey availability covaried with the owl's annual reproductive output, the available biomass of mice and voles *(r* = 0.78, *P* = 0.07), of all five common prey species *(r* = 0.78, *P* = 0.06), and of all five common prey species occupying the mesic forest habitat *(r* = 0.76, *P* = 0.08). Correlations with all other variables describing prey availability, habitat condition, or weather were weak or unapparent *(r* < 0.7 and *P* > 0.10; Table 3.8). Whereas each of the mouse or vole species showed a positive (but statistically insignificant) relationship with the owl's annual reproductive output, the available biomass of woodrats showed no correlation (Table 3.8). In fact, when the available biomass of woodrats is removed from consideration (Fig 3.8a versus 3.8b), there is little effect on the correlation with owl reproduction. During the study period, the trend in reproduction by Mexican spotted owls in the Sacramento Mountains showed little correspondence with available biomass of woodrats (Fig 3.8c).

DISCUSSION

In this chapter, I examined dietary and reproductive responses of Mexican spotted owls to variation in their common prey using an observational approach. I also examined the relative influence of two other potentially key factors on the owl's reproduction; weather and habitat. I relied upon temporally related factors to induce discernable change in the owl's food resources and energetic needs while monitoring a concurrent response in the owl's diet and reproduction. Estimates of prey consumption and availability varied enough over 6 years of study to permit quantitative tests for prey selection, switching, and preference, and for describing average functional and short-term numerical responses

within this spotted owl population.

Following initial description of the owl's diet, I narrowed common food resources to three prey types, mice, voles, and woodrats, which were comprised of five species (deer mouse, brush mouse, Mexican vole, long-tailed vole, and Mexican woodrat). Other species were consumed and undoubtedly contributed to the owl's energetic and nutritional needs. Examination of five common species analyzed here as three genera, however, was sufficient to demonstrate key properties of this owl's reaction to highly variable food supplies and energetic demands.

Temporal trends in availability of the owl's common prey were moderately dynamic and varied according to prey type. Degree of temporal variation corresponded inversely with prey size. Mouse and vole availability were substantially variable over time, primarily due to periodic irruptions of deer mice in mesic forests and both species of voles in montane meadows. In contrast, availability of Mexican woodrats varied only slightly during the 6 years of study and abundance of this species was roughly equivalent in the two forested habitats. Trend patterns also varied among these prey. Available biomass of mice and voles were mildly synchronous in time whereas biomass of mice and woodrats were asynchronous.

Patterns of prey consumption mimicked those previously established for this population of Mexican spotted owls. Relative frequencies of mice consumed by these Mexican spotted owls averaged over six breeding seasons (1994–1996) were slightly lower (34% vs. 40%) compared to those previously reported from the 1991–1993 breeding seasons (Ward and Block 1995). Relative frequencies of voles (22% vs. 20%) and woodrats (11% vs. 8%) were slightly higher but similar. Patterns of percent biomass

consumed were also similar (mice 15% vs 12%; voles 16% vs.12%; woodrats 25% vs. 20%).

According to mean relative frequencies in this study, mice and voles were taken most often; woodrats were consumed much less frequently. According to mean biomass, woodrats contributed more to the owl's food habits than any other prey type, but still in lesser amounts than have been reported for northern portions of this subspecies' range or for the other two spotted owl subspecies (Gutiérrez et al. 1995, Ward and Block 1995). Given the 6-year averages of percent biomass consumed, woodrats could be considered a primary prey for these owls. However, maximum percentage of woodrat biomass consumed by these owls was <40% during any one breeding season, highlighting a potential need for alternative prey.

Understanding the owl's dietary response relied not on the 6-year averages of relative consumption but on the variation in consumption, prey availability, and the owl's energetic needs. Scrutiny of temporal trends in these conditions revealed that functional responses by members of this spotted owl population varied significantly according to prey type. Woodrats were selected consistently, whereas mice and voles were usually avoided or taken in accordance with their availability. When woodrats were less available, Mexican spotted owls tended to select voles. However, the switch to voles was partially mitigated by availability and consumption of mice. For example, trends of prey selection in Figure 3.5 showed that when woodrat biomass was least available (25 kg / owl foraging range) during the breeding season of 1991, consumption of vole biomass was less than expected given its availability. Thus, during 1991, these owls did not switch to voles as would be predicted by theory developed for systems with only two prey

species (i.e., vole selection should have been >1 for switching to have occurred; Murdoch 1969, Real 1990). Concurrently, though, consumption and availability of mouse biomass (282 kg / owl foraging range) was greater than during other breeding seasons. In 1994, woodrat biomass was also low (33 kg / owl foraging range) but unlike 1991, mouse biomass was reduced to moderate levels (91 kg / owl foraging range) and consumption of mice by these owls followed suit. However, this time vole selection was significantly >1 and indicated switching by owls to voles. Apparently, these spotted owls switched to voles only when the other two prey were limited.

By accounting for food surplus, and by implication the potential for owls to be satiated, the relative preference among these prey types was clarified further (e.g., Fig. 3.6). Owls selected woodrats increasingly as food surpluses increased, indicating a strong preference for this prey. Selection of mice was not affected by changes in food surpluses, whereas voles were selected during periods when surpluses were low and their selection by owls diminished disproportionately with increasing surpluses. Thus, within this assemblage of common prey, voles were probably preferred least and mice secondarily to woodrats.

Reliability of these findings rests primarily on the validity of two measures, prey consumption and availability. Procedures for identifying and quantifying diet composition from regurgitated pellets followed other studies of owl food habits and were generally reliable (Marti 1987). I reduced bias associated with misidentification of pellet remains by using general groupings and by analyzing data at the genus level. However, population-level inferences about diet composition necessitated that sampling of food items within and among territories was representative and variation among individuals

was low. I assumed that opportunistic sampling was a random process and therefore provided a reliable means for estimating dietary proportions (Marti 1987, Petty 1999). To my knowledge, this assumption has never been thoroughly tested for species like spotted owls that use multiple roosts during the breeding season, and it warrants further consideration. Given the assumption that my samples of food remains were approximately random, then variability in consumption of common prey among owl family units was shown to be reasonably low (CV <22%). This amount of variation was similar to interterritorial variation in woodrat consumption by California spotted owls (Smith et al. 1999).

Reliability of estimates of available prey depended on unbiased and precise estimation of habitat-specific amounts of prey abundance and on amounts of these habitats in the owls' foraging ranges. Both of these variables were sampled with rigor and estimation was based on modern estimators (See also Chapter 2 and Appendix 3.B). Assumptions regarding the use of circular areas for estimating amounts of foraging habitat were tested and found to be very similar to composition within a subsample of measured home ranges. Nonetheless, precision of small rodent density was probably biased during years of low abundance and for all estimates of woodrat density (White et al. 1982, Menkens and Anderson 1988). This could render significant selection ratios that were close to 1.0 in specific years insignificant. However, the primary emphasis in this chapter was on quantifying and comparing response trends to identify key prey species. Interpretation of multi-annual trends would be less affected by this form of imprecision.

Clarity of the functional responses was greatly dependent on the magnitude of

change in prey populations. Limited change in this observational study would be analogous to a small range of treatment affects in a controlled experiment. Populations of deer mice and both vole species experienced irruptions during the 6-year period, leading to a reasonable and natural range of change for documenting response to these prey (see also Chapter 2). Abundance in Mexican woodrat populations, however, remained low and comparatively stable though out the study. This raises the question as to whether low woodrat numbers were limited by inadequate sampling or by ecological process.

Evidence suggests that low abundance of Mexican woodrats was real and a function of ecological process. Low densities of Mexican woodrats seem consistent with most other studies of woodrat abundance. For example, summer densities of Mexican woodrats in this study ranged from 0.44–1.18 individuals/ha in mesic forests and from 0.70–2.07 individuals/ha in xeric forests over a 6-year period. Only one other study (Goodwin and Hungerford 1979) has reported estimates of absolute abundance of Mexican woodrats. They reported summer ecological densities of Mexican woodrats of 4.9–24.7/ha in rocky canyons of ponderosa pine forest, northern Arizona, and 4.9–27.2/ha in manipulated forest treatments with slash piles. Ecological densities (number of individuals per unit of area of suitable habitat) typically overestimate crude densities. Thus, the greater densities in the later study are in large part due to division by a smaller unit of area, rather than increased numbers. Estimates of relative summer abundance of Mexican woodrats were found to be low compared to other commonly trapped rodents, ranging from 0.2–0.3 individuals/100 trap-nights in canyon woodlands in southeastern Utah (Sureda and Morrison 1998). Similarly, the majority of studies on other woodrat species have reported low densities ranging from 0.2–4.2 individuals/ha (Linsdale and

Tevis 1951, Chew and Chew 1970, Sakai and Noon 1993, Ward et al. 1998, Carey et al. 1999). An exception is abundance of dusky-footed woodrats (*N. fuscipes*) occurring in oak or shrub dominated habitats of California, where dense populations (8.2–81.1 individuals/ha) occur (Linsdale and Tevis 1951, Sakai and Noon 1993). Only Linsdale and Tevis (1951) have reported multi-annual trends in absolute woodrat abundance, finding that over four consecutive springs (1939–1942) a population of dusky-footed woodrats varied only 11% from its mean abundance. Thus, the sparse and mildly fluctuating numbers I documented here for Mexican woodrat populations were probably real and not an artifact of inadequate sampling procedures.

One alternative explanation is that preferred predation by Mexican spotted owls has suppressed Mexican woodrat populations within the owl's foraging habitat. Although predators generally cannot prevent irruptions of prey once they begin, it is possible that predation can stabilize prey numbers following a population decline. For example, lynx (*Lynx lynx*), dingo (*Canis familiaris dingo*), and several avian predator populations have suppressed populations of their primary prey when alternative prey were abundant enough to support these predators' persistence (Pearson 1964, Bergerud 1983, Corbett and Newsome 1987, Jaksić et al. 1992). A second, but not mutually exclusive explanation, is that habitat quality for woodrats in mesic forests has simultaneously diminished with successional increase of pole-sized conifer trees and loss of food plants or den structures, thereby limiting the woodrat's population growth (see Chapter 2).

Other moderate- to long-term studies of spotted owl food habits conducted in conjunction with knowledge of prey availability have not been published. However, annual trends in food habits and, in some cases, prey availability from European studies

of similar *Strix* species provide a basis for comparison. Like members of this population of Mexican spotted owls, Ural owls (*S. uralensis*) and tawny owls (*S. aluco*) both are forest or woodland residents and generalist feeders on a variety of small mammals (Korpimäki 1986). Ural owls are larger (average male mass = 720 g; female mass = 821 g; Mikkola 1983) than Mexican spotted owls (average male mass = 509 g; female mass = 569 g; Gutiérrez et al. 1995), whereas tawny owls are smaller (average male mass = 449 g; female mass = 554 g; Mikkola 1983). Prey relationships documented from Mexican spotted owls in this study were most similar to those reported for Ural owls. These owls consume small (~25 g) rodents like field (*Microtus agrestis*) or common voles (*M. epiroticus*) more frequently than other prey by number and in accordance with their abundance while consuming more biomass of the larger (177 g) water vole (*Arvicola terrestris*) (Lundberg 1981, Korpimäki and Sulkava 1987, Korpimäki et al. 1990). Lundberg (1981) further suggested that consumption of field voles was dependent upon availability of the larger water vole.

Tawny owls typically consume smaller rodents like yellow-necked field or wood mice (*Apodemus flavicollis*; *A. sylvaticus*) and bank voles (*Cletrionomys glareolus*) in correspondence with their availability (Southern 1954, Nilsson 1984, Jedrzejeski et al. 1996). However, during a 20-year study in Berlin, Germany, Wendland (1984) found a distinct asynchrony in the proportion of birds and yellow-necked field mice consumed and suggested that tawny owls switched to birds when their preferred prey were less available. More recently, Petty (1999) has shown that field voles were the most important prey for tawny owls in northern England, where silviculture has reduced availability of wood mice and bank voles. Combined, these studies show that while some

forest-dwelling *Strix* owls may prefer larger nocturnal rodents when available there is also a capacity to switch among prey types and to use smaller rodents in relation to their availability in an opportunistic fashion.

In the present study, both analytical forms of functional responses indicated that Mexican spotted owls took small prey such as mice and voles opportunistically. For example, relative functional responses showed that consumption of mice and voles was linear, simply reflecting proportional availabilities over a wide range of abundances. The absolute functional response to mice was also linear (Type I of Holling 1959), indicating opportunistic use by the owls. The absolute functional response to voles, however, was curvilinear (Type II of Holling 1959), indicating that the opportunism had limits, likely because meadow dwelling voles cannot be accessed by spotted owls as readily as can forest-dwelling mice.

In generalizing Holling's (1959) models of functional response, Fujii et al. (1986) stated that the strictly linear response was not feasible, that the response must plateau. While I agree with these authors that the response should eventually become asymptotic, I have shown that this owl's absolute response to the combined abundance of two mouse species was indeed linear and over a very wide range of abundance (2,100 to 17,100 mice per owl foraging area). Linear functional responses by diurnal Australian raptors to irrupting house mouse (*Mus musculus*) populations have also been reported (Sinclair et al. 1990). Most functional responses observed from owls have fit Holling's (1959) Type II model, and most of these were responses to cyclic vole populations (Phelan and Robertson 1978, Korpimäki and Sulkava 1987, Korpimäki and Norrdahl 1991, Rohner et al. 1995, Jedrzejewski et al. 1996, Petty 1999). Thus, there is additional evidence that a

linear response is possible but that it may be restricted to situations where readily accessible prey, like mice, irrupt periodically.

Relative functional response toward woodrats was also linear but the form was less precise compared to the smaller prey and it showed strong selection for this species over a narrow range of availability. In contrast, the absolute functional response to woodrats was convex in form. This type of response was not originally predicted by Holling (1959). However, Fujii et al. (1986) stated that distraction by other prey or changes in dispersion concomitant with increases of the targeted prey may cause "humped" shaped responses. Either was likely in this study. For example, far less woodrat biomass was consumed than expected when available woodrat biomass was at its greatest in 1992. Concurrently, long-tail and Mexican voles were at peak numbers and were consumed in moderately high amounts. Thus, assuming the curve is not simply an artifact of small sample size, it is possible that more attention to voles caused this type of response in Mexican spotted owls. An alternative explanation is that clumping of Mexican woodrats occurred with increases in density and social behavior associated with clumping provided some protection from predation by spotted owls. Linsdale and Tevis (1951) have shown that young dusky-footed woodrats tend to colonize near existing houses, forming a clumped distribution. However, it is unknown if this applied to Mexican woodrats in the Sacramento Mountains and whether their social behavior would permit escape from predation.

Is selection of Mexican woodrats optimal behavior for Mexican spotted owls? The answer to this question must address the effects of prey use on the owl's fitness. Existing studies have not shown strong relationships between proportions of specific prey

consumed by this owl and its reproductive output (Ward and Block 1995, Seamans and Gutiérrez 1999). In addition, the relationship between consumption of different prey types and the owl's survival has not been quantified.

Although an extensive body of theory exists for predicting optimal diet selection (see reviews by Pyke 1984, Real 1990), I did not test this idea directly for lack of germane parameters. For example, optimal prey selection is believed by some to maximize fitness when energy gained is maximized per unit of foraging effort (Pyke 1984). Testing this hypothesis requires data on profitability of prey as measured by its energetic reward after accounting for rates of prey encounter, handling, and capture by Mexican spotted owls. Although some indication of energetic reward (via size) and capture rate is given here, profitability could not be fully estimated because search times, handling times, and encounter rates were not available for the owl's common prey. Physiological state of the foraging organism and its perceived risk to predation are also important parameters for understanding the optimality of prey choice (Houston 1990; 1993, McNamara 1990). In this study, selectivity by Mexican spotted owls for a large, energetically rewarding prey was
greatest when the owl's food surplus was greatest, and this initial analysis would appear counter to optimal foraging behavior.

Finding that woodrats were preferred by these owls but not finding any association between availability of this prey and the owl's reproduction was also contrary to prediction. Models of reproductive potential and trends in temporal covariation showed that availability of mice and voles exerted a stronger influence on reproduction. In the Sacramento Mountains, spotted owls produced more young when mice and/or

voles were more abundant. Several studies in Europe or Fennoscandia have also shown that several medium-sized owl species either forgo nesting or produce few young when voles or mice are limited in number during late spring (Southern 1970, Lundberg 1976, Korpimäki and Norrdahl 1991, Korpimäki 1992). However, the availability of medium-sized, nocturnal rodents was not well documented in these studies, making it difficult to assess the selection of larger prey.

Why wouldn't availability of preferred prey be correlated with this predator's reproductive success? At first glance, the pattern seems maladaptive. However, because the owl's fitness is also a function of survival, maintenance energy must be acquired before an owl can reproduce. Thus, the effect of woodrat availability on reproduction may be more subtle than can be demonstrated by correlation analyses. Franklin et al. (2000) have pointed out that, as with many owl species, life-history traits of spotted owls represent a "bet-hedging" strategy. If woodrats can supply a relatively consistent food base, then preference for this rodent may have evolved because it permits survival and the opportunity to reproduce when conditions permit. Over the 6 years of study in the Sacramento Mountains, spotted owls reproduced when prey smaller than woodrats were abundant. In other regions where spotted owls consume predominately woodrats, both survival and reproduction may be influenced directly by this preferred prey. This does not appear to be the case for Mexican spotted owls occurring in the Sacramento Mountains.

One alternative explanation is that the owl's prey selection behavior is remnant from a time when woodrats were more abundant, and hence provided enough biomass to stimulate the owl's reproduction. Mixed-conifer forest is the most abundant forest type

found in proximity to roost centers and nest sites. However, as a consequence of timber harvest, much of the remaining mixed-conifer forest is comprised of a mid-seral stage 60–100 yrs in age (Kaufmann et al. 1998). Thus, the structure of significant amounts of the owl's present-day foraging habitat has changed to a younger, denser forest. Limited evidence presented in Chapter 2 shows that in some years, late-seral forest has greater abundance of woodrats and long-tailed voles and fewer deer mice than in the mid-seral condition. Thus, in a former landscape with more late-seral foraging habitat and more woodrats, Mexican spotted owls in the Sacramento Mountains may have evolved a preference because woodrats were at that time abundant enough to stimulate reproduction. Spotted owls may have persisted in the Sacramento Mountains despite such rapid large-scale alteration of their habitat because earlier seral stages may have also triggered periodic irruptions of an alternative prey. The predator-prey relationships uncovered in this system may in part be the consequence of past habitat alteration.

Another explanation is that other factors confounded the correlation between woodrat availability and reproduction. Other studies of spotted owls have found that adult females have greater fecundity than subadult females (Forsman et al. 1996, Seamans et al. 1999). Although the ages of Mexican spotted owls sampled during this study were undocumented, it is unlikely that the great variation in annual reproductive output was caused entirely by temporal shifts in the age distribution of this population. Reproduction in a given year may also be affected by reproduction in a previous year (Wagner et al. 1996). However, the temporal trend in reproduction of the Sacramento Mountain population did not exhibit a saw-toothed pattern characteristic of this effect.

Severe weather could also disrupt reproduction despite ample woodrat numbers.

However, weather effects on reproduction described recently for northern and California spotted owls (Franklin et al. 2000, North et al. 2000) were either weak or undetectable for this population of Mexican spotted owls. Though three weather variables were found relatively important in modeling the owl's reproductive potential, they explained little overall variation among owl territories and did not covary significantly with the owl's annual reproductive output. Thus, it is doubtful that a prominent weather factor like rain during the nesting season corrupted any association between availability of woodrats and Mexican spotted owl reproduction. The limited influence of spring precipitation on Mexican spotted owl reproduction may be explained by lack of significant amounts of precipitation during this time. Regions where the effect has been uncovered typically receive 21–27 cm during the nesting period (March–May) whereas the Sacramento Mountains receive only 4–15 cm during this time.

In summary, the lack of correlation between the owl's preferred prey, Mexican woodrats, and its reproduction does not appear to be confounded by other influences. Correlations with the four other common prey species with the owl's reproductive output were also not statistically significant but the association with deer mice and long-tailed voles was stronger than the other species. Not until the combined biomass of all common prey was considered did the correlation approach significance. If the conservation goal is to maintain the current spotted owl-prey relationships, then this finding suggests that providing for a diverse prey base is a valid objective, as previously recommended (Ward and Block 1995). The findings here also suggest that the assemblage of prey within the mesic forest habitat (predominately mixed-conifer forest type) available to foraging owls exerts the greatest influence on this owl's reproduction. Hence, conditions within this

habitat type should be a conservation priority.

Unlike some studies of northern spotted owls (Bart and Forsman 1992, Ripple et al. 1997), I found no relationship between amount of particular habitat and the owl's reproduction. Analysis of different land-areas could explain the different results (e.g., see discussion by Meyer et al. 1998). I chose to analyze habitat amounts within circular areas the size of an average breeding-season home range (radius = 1.2 km) because this scale is most likely to show relationships between habitat condition and measures of population performance (Raphael et al. 1996). This size of land-area was smaller than the landscape scales examined in these other studies. Also, as categorized, the amounts of these broad habitat types in areas settled by spotted owls in the Sacramento Mountains changed very little over time, whereas populations of several prey species were dynamic. However, once I considered the amount of common prey biomass in a particular habitat type, I found a positive association between prey in the mesic forest type and the owl's reproduction. Consequently, in this study, habitat type alone did not provide a surrogate measure of prey condition for modeling reproduction by spotted owls.

Lack of macrohabitat-correlates with reproductive potential may also be explained by lack of variation in habitat composition of foraging areas. If the landscape occupied by Mexican spotted owls during the study area was not saturated, then foraging owls may have hunted over a similar mosaic of habitats. That is, in the absence of density-dependent effects a gradient in quality among foraging areas may be less pronounced. Low variation in dietary measures and amounts of mesic forest ($\bar{x}$ = 331 ha, CV = 25%) among owl territories supports this point. A similar effect may result from extensive deforestation and rapid succession that homogenizes the landscape with large tracts of

even-aged forest.

Conservation implications of these findings depend on knowledge of both functional and numerical responses. From the dietary responses and patterns of prey availability described above, the following points can be made. First, a focus on increasing the availability of Mexican woodrats may invoke the most efficient uptake of energy into this Mexican spotted owl population. Abundance of this rodent was apparently limited in the owl's foraging areas. The owl's great preference and functional response toward this species suggests that a moderate increase in the amount of Mexican woodrats would produce a maximal increase in consumption of this prey. Second, the strong linear response to mice might suggest increases in deer mouse and brush mouse populations as another management target. However, opportunistic use of this widely occurring prey by the owl may occur naturally enough that purposeful manipulations would prove futile. Designs to increase vole numbers may also prove inefficient for similar reasons. When vole populations attained peak numbers in portions of the owl's foraging habitat, the owl's ability to capitalize on such increases was limited. Although selection of voles was greatest by these owls when food surpluses were lowest, signaling a temporary but strong need for this prey, increased availability of woodrats might diminish this need. Thus, strategies designed to increase woodrat availability by increasing shrub diversity and den sites (see Chapter 2) appear to be the most logical given the owl's feeding behavior.

Given a strong association between the owl's reproductive output and available biomass of mice and voles, one could argue that a productive strategy would be to increase populations of these smaller prey. However, reliance by spotted owls on mice

and voles, which often undergo dynamic fluctuations during a an owl's lifetime, may be contributing to high temporal variance in the owl's reproduction and recruitment. This point, other potential ramifications of these management options, and associated research directions are discussed in Chapter 4.

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Table 3.1. Temporal and spatial replication of small mammal abundance in the Sacramento Mountains, New Mexico (1991–1996).

	Sites Sampled By Year[a]					
Habitat	1991	1992	1993	1994	1995	1996
Mid-seral	BLUF	DELW	DELW	DELW	DELW	DELW
Mesic Forest	GRES	HAYC	HAYC	HAYC	HAYC	
		ZINK	ZINK	ZINK	ZINK	
		WAYL	WAYL	WAYL		
		WIWH	WIWH	WIWH		
		LWIL	LWIL			
Total:	2	6	6	4	3	1
Montane		DELW	DELW	DELW	DELW	DELW
Meadow		HAYC	HAYC	HAYC	HAYC	
		WILL	WILL	WILL	WILL	
		LWIL	LWIL	LWIL		
		WAYL	WAYL	WAYL		
		WIWH	WIWH	WIWH		
Total:	0	6	6	6	3	1
Xeric Forest	$FIRE_1$	JAMS	JAMS	JAMS	JAMS	JAMS
	SIXT	CARR	CARR	CARR	CARR	
		DRYB	DRYB	DRYB	BRYB	
		$FIRE_2$	$FIRE_2$	$FIRE_2$		
		TRAL	TRAL	TRAL		
		WALK	WALK	WALK	WALK	
Total:	2	6	6	6	4	1

[a] Site names and universal transverse mercator coordinates (zone 13) for center of trapping grid: BLUF–Bluff Springs (4303E, 36321N); CARR–Carr Gap (4547E, 36438N); DELW–Delworth (MF:4309E, 36330N; MM:4305E, 36324N); DRYB–Dry Burnt (4473E, 36458N); $FIRE_1$–Fire 1(4552E, 36450N); $FIRE_2$–Fire 2 (4547E, 36446N); GRES–Greasy Canyon (4418E 36328N); HAYC–Hay Canyon (MF:4396E, 36295N; MM:4393E, 36298N); JAMS–James Canyon (4447E, 36474N); LWIL–Lower Wills Canyon (MF:4338E, 36311N; MM:4331E, 36311N); SIXT–Sixteen Springs (4541E, 36491N); TRAL–Trail Canyon (4444E, 36215N); WALK–Walker (4521E, 36474N); WAYL–Wayland (MF:4375E, 36237N; MM:4375E, 36239N); WILL–Upper Wills Canyon(4304E, 36293N); WIWH–Willie White Canyon (MF:4322E, 36324N; MM:4313E, 36323N); ZINK–Zink Trick (4372E, 36513N).

Table 3.2. Models predicting influences of prey availability, weather, or habitat type on reproductive potential (RP) of Mexican spotted owls in the Sacramento Mountains, New Mexico (1991–1996). Original models were developed *a priori* from relationships indicated in published literature. Exploratory models were developed following examination of results from original models.

Model Set / Acronym	Model Structure[a]	Implied Effects on Owl Reproductive Potential
Original / Global	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet NEMEA + \beta_4 \bullet PEMAA + \beta_5 \bullet PEBOA + \beta_6 \bullet MILOA + \beta_7 \bullet MIMEA$	Colder temperatures during preceding fall and winter increases energetic demand; excessive rain during nest season increases energetic demand, lowers accessability to prey, and leads to nest abandonment; reproduction is greater when Mexican woodrats, deer mice, brush mice, long-tailed voles, and Mexican voles are more abundant in the male owl's foraging range.
C1	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet NEMEA$	Cold fall-winter temperatures and rain during nesting period have a negative influence; availability of Mexican woodrats has a positive influence.
C2	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet PEMAA + \beta_4 \bullet PEBOA + \beta_5 \bullet MILOA + \beta_6 \bullet MIMEA$	Cold fall-winter temperatures and rain during nesting period have a negative influence; availability of mice and voles has a positive influence.
C3	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet PEMAA + \beta_4 \bullet PEBOA$	Cold fall-winter temperatures and rain during nesting period have a negative influence; availability of mice has a positive influence.
C4	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet MILOA + \beta_4 \bullet MIMEA$	Cold fall-winter temperatures and rain during nesting period have a negative influence; availability of voles has a positive influence.
C5	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet MFPREY$	Cold fall-winter temperatures and rain during nesting period have a negative influence; availability of common prey in mesic forest has a positive influence.

Table 3.2. (Continued).

Model Set / Acronym	Model Structure[a]	Implied Effects on Owl Reproductive Potential
Original / C6	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet MFHA$	Cold fall-winter temperatures and rain during nesting period have a negative influence; amount of mesic forest in male owl's foraging range has a positive influence.
C7	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN$	Cold fall-winter temperatures and rain during nesting period have a negative influence.
C8	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet PFSRAIN$	Cold temperatures during the fall-winter period and total rainfall during preceding fall-spring period have a negative influence.
C9	$RP = \beta_0 + \beta_1 \bullet ENTEMP - \beta_2 \bullet NSTRAIN$	Cold temperatures during early nest period (April)and rain during nesting period have a negative influence.
C10	$RP = \beta_0 + \beta_1 \bullet ENTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet COMPA$	Cold temperatures during early nesting period and rain during nesting period have a negative influence; availability of five common prey have a positive influence.
C11	$RP = \beta_0 + \beta_1 \bullet ENTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet SMLPA$	Cold temperatures during early nesting period and rain during nesting period have a negative influence; availability of mice and voles have a positive influence.
C12	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet COMPA$	Cold fall-winter temperatures and rain during nesting period have a negative influence; availability of five common prey has a positive influence.
C13	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet SMLPA$	Cold fall-winter temperatures and rain during nesting period have a negative influence; availability of mice and voles has a positive influence.

Table 3.2. (Continued).

Model Set / Acronym	Model Structure[a]	Implied Effects on Owl Reproductive Potential
Original / C14	$RP = \beta_0 + \beta_1 \bullet FWTEMP - \beta_2 \bullet NSTRAIN + \beta_3 \bullet HABEV$	Cold fall-winter temperatures and rain during nesting period have a negative influence; diversity (evenness) of habitat in male owl's foraging area has a positive influence.
C15	$RP = \beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet COMPA$	Cold fall-winter temperatures have a negative influence; availability of five common prey has a positive influence.
C16	$RP = \beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet SMLPA$	Cold fall-winter temperatures have a negative influence; availability of common small prey has a positive influence.
C17	$RP = \beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet MFHA$	Cold fall-winter temperatures have a negative influence; amount of mesic forest has a positive influence.
C18	$RP = \beta_0 + \beta_1 \bullet FWTEMP + \beta_2 \bullet HABEV$	Cold fall-winter temperatures have a negative influence; diversity of habitat has a positive influence.
C19	$RP = \beta_0 + \beta_1 \bullet COMPA$	Availability of five common prey has a positive influence.
C20	$RP = \beta_0 + \beta_1 \bullet SMLPA$	Availability of mice and voles has a positive influence.
C21	$RP = \beta_0 + \beta_1 \bullet MFPREY$	Availability of five common prey in the mesic forest has a positive influence.
C22	$RP = \beta_0 + \beta_1 \bullet MFHA$	Amount of mesic forest in male owl's foraging area has a positive influence.
C23	$RP = \beta_0 + \beta_1 \bullet HABEV$	Habitat diversity in male owl's foraging area has a positive influence.

Table 3.2. (Continued).

Model Set / Acronym	Model Structure[a]	Implied Effects on Owl Reproductive Potential
Exploratory /		
E1	$RP = \beta_0 - \beta_1 \bullet NSTRAIN + \beta_2 \bullet SMLPA$	Rain during nesting period has a negative influence and availability of mice and voles has a positive influence.
E2	$RP = \beta_0 - \beta_1 \bullet NSTRAIN + \beta_2 \bullet COMPA$	Rain during nesting period has a negative influence and availability of woodrats, mice and voles has a positive influence.
E3	$RP = \beta_0 - \beta_1 \bullet NSTRAIN + \beta_2 \bullet MFPREY$	Rain during nesting period has a negative influence and availability of woodrats, mice and voles in mesic forest habitat has a positive influence.
E4	$RP = \beta_0 - \beta_1 \bullet SNSTRAIN + \beta_2 \bullet SSMLPA$	Same effects as implied in Model E1; regressor data represent cumulative sums from owl territories rather than mean values.
E5	$RP = \beta_0 - \beta_1 \bullet SNSTRAIN + \beta_2 \bullet SCOMPA$	Same effects as implied in Model E2; regressor data represent cumulative sums from owl territories rather than mean values.
E6	$RP = \beta_0 - \beta_1 \bullet SNSTRAIN + \beta_2 \bullet SMFPREY$	Same effects as implied in Model E3; regressor data represent cumulative sums from owl territories rather than mean values.
E7	$RP = \beta_0 - \beta_1 \bullet NSTRAIN$	Rain during nesting period has a negative influence.
E8	$RP = \beta_0 + \beta_1 \bullet ELEV + \beta_2 \bullet ELEV^2$	Maximum reproduction is achieved at a mid-range of elevations occupied by members of this owl population.

[a] Regressor variables are further defined in text.

Table 3.3. Relative frequency (%) of prey items found in pellets regurgitated by Mexican spotted owls occurring in the Sacramento Mountains, New Mexico, during the breeding seasons (1 March to 31 September) of 1991–1996.

	1991		1992		1993		1994		1995		1996		1991–1996 [b]		
Prey [a]	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	CV_S	CV_Y
Shrews	2.1	0.67	2.7	1.16	2.8	1.05	2.7	2.70	0	—	4.1	1.66	2.4	10.5	0
Bats	0.5	0.34	0	—	0.6	0.26	4.2	4.17	0	—	0	—	0.9	15.6	0
Rabbits	3.0	0.84	8.0	4.10	3.7	0.89	3.4	1.99	9.6	4.58	6.4	2.39	5.7	14.9	0
Squirrels/chipmunks	1.2	0.91	1.0	0.79	0.6	0.32	2.5	1.75	1.5	1.52	2.0	0.74	1.5	30.0	0
Botta's pocket gopher	1.4	0.79	5.1	1.68	2.3	0.67	3.7	1.74	9.4	2.77	6.9	1.82	4.8	27.1	54.9**
White-footed mice	53.7	4.41	21.7	8.54	17.5	2.79	48.2	6.99	28.9	7.84	35.9	4.95	34.3	17.5	39.0**
Woodrats	8.4	1.18	5.9	2.35	7.9	1.89	7.8	1.27	20.5	3.31	16.1	2.16	11.1	21.0	47.6**
Voles	14.8	2.76	25.5	6.43	33.4	4.38	21.1	5.53	17.3	4.75	19.0	2.09	21.8	13.1	25.1*
Medium-sized mammals	3.6	1.31	5.7	1.90	7.7	2.86	0.9	0.93	0	—	0.8	0.83	3.1	37.1	65.8**
Small mammals	0.4	0.24	1.7	1.11	6.1	2.05	0	—	3.3	3.33	0	—	1.9	51.1	69.0**
Birds	3.0	0.68	3.3	1.36	2.7	0.67	5.5	3.93	3.1	1.40	4.1	1.40	3.6	6.8	0
Arthropods	8.0	1.65	19.4	8.49	14.8	2.54	0	—	6.4	2.55	4.7	1.19	8.9	32.5	39.4**
Total:	100.0		100.0		100.0		100.0		100.0		100.0		100.0		
No. owl territories:	17		9		15		4		6		11		62		
Items per territory [c]:	10-77		10-70		11-173		12-37		11-17		11-36				

[a] Scientific names of identified species are given in Appendix 3.E. Medium-sized (>50 g) and small mammal categories included remains identified to species belonging to higher taxa not listed or mammal remains that could not be identified beyond class and size.

[b] CV_S = coefficient of variation in the owl's diet attributed to sampling variation within and among owl territories (%); CV_Y = coefficient of variation in the diet among breeding seasons (%); * and ** indicate that annual variation in consumption of this prey is significant at the 0.05 or 0.001 level, respectively.

[c] Range (after all samples <10 items were discarded).

Table 3.4. Percent biomass of prey found in pellets regurgitated by Mexican spotted owls occurring in the Sacramento Mountains, New Mexico, during the breeding seasons (1 March to 31 September) of 1991–1996. Prey mass and associated sources are given in Appendix 3.F.

	1991		1992		1993		1994		1995		1996		1991–1996 [b]		
Prey [a]	c̄	SE	c̄	SE	c̄	SE	c̄	SE	c̄	SE	c̄	SE	c̄	CV_S	CV_Y
Shrews	0.4	0.14	0.4	0.15	0.5	0.19	0.5	0.46	0	—	0.6	0.27	0.4	8.0	0
Bats	0.1	0.11	0	—	0.2	0.10	2.0	2.03	0	—	0	—	0.4	18.3	0
Rabbits	13.3	3.48	27.6	10.61	13.0	3.01	12.9	7.71	22.6	10.32	18.1	4.82	17.9	10.3	0
Squirrels and chipmunks	3.5	1.99	9.8	3.24	4.9	1.27	8.9	4.74	14.8	4.95	11.6	2.62	4.0	24.0	0
Botta's pocket gopher	3.9	2.55	2.4	1.94	2.4	1.49	8.5	5.11	1.6	1.56	5.6	2.19	8.9	21.7	37.9*
White-footed mice	29.7	3.60	9.1	3.73	8.5	1.49	21.0	4.19	8.8	2.69	14.1	3.26	15.2	23.4	52.9**
Woodrats	25.3	3.39	14.5	4.82	18.7	3.87	21.6	1.85	39.9	6.15	31.1	3.34	25.1	13.9	30.0**
Voles	11.0	1.83	17.4	4.41	26.4	4.37	17.2	5.64	9.5	3.27	12.0	1.42	15.6	16.7	33.5**
Medium-sized mammals	8.7	3.07	13.1	4.58	15.9	3.77	2.2	2.20	0	—	2.6	2.61	7.1	31.8	57.5*
Small mammals	0.2	0.13	0.5	0.31	4.6	1.92	0	—	1.5	1.45	0	—	1.1	66.9	90.7**
Birds	3.6	0.86	4.4	1.71	4.5	1.71	5.2	3.17	1.7	0.78	4.1	1.22	3.9	15.8	11.6
Arthropods	0.2	0.05	0.8	0.54	0.4	0.08	0	—	0.1	0.03	0.1	0.03	0.3	43.0	92.4**
Total:	100.0		100.0		100.0		100.0		100.0		100.0		100.0		
No. owl territories:	17		9		15		4		6		11		62		
Items per territory [c]:	10-77		10-70		11-173		12-37		11-17		11-36				

[a] Scientific names of identified species are given in Appendix 3.E. Medium-sized (>50 g) and small mammal categories included remains identified to species belonging to higher taxa not listed or mammal remains that could not be identified beyond class and size.

[b] CV_S = coefficient of variation in the owl's diet attributed to sampling variation within and among owl territories (%); CV_Y = coefficient of variation in the diet among breeding seasons (%); * and ** indicate that annual variation in consumption of this prey is significant at the 0.05 or 0.001 level, respectively.

[c] Range (after all samples <10 items were discarded).

Table 3.5. Ratios (w_i) of proportions of prey consumed (o_i) to proportions of prey available (π_i) used to quantify prey selection by Mexican spotted owls during six breeding seasons (1991–1996) in the Sacramento Mountains, New Mexico. Statistical significance is based on Bonferroni adjustments for multiple, simultaneous comparisons. Prey taken in significantly greater proportions than available compared to other prey species (indicated as '+') are inferred to be selected. Two sets of ratios are given for each prey genera, one estimated from prey frequency and another from prey biomass.

Measure /		Mice (*Peromyscus* spp.)					Voles (*Microtus* spp.)					Woodrats (*Neotoma* spp.)				
Year	χ^2 [a]	o_i	π_i	w_i	95% CI [b]		o_i	π_i	w_i	95% CI		o_i	π_i	w_i	95% CI	
Frequency																
1991	172.7	0.71	0.69	1.029	0.947–1.111	o	0.17	0.30	0.561	0.406–0.717	–	0.12	0.01	14.103	9.179–19.026	+
1992	28.8	0.37	0.25	1.458	1.113–1.804	+	0.53	0.71	0.747	0.621–0.874	–	0.11	0.04	2.499	1.192– 3.807	+
1993	45.8	0.33	0.48	0.691	0.586–0.797	–	0.54	0.44	1.211	1.091–1.331	+	0.14	0.08	1.668	1.217– 2.119	+
1994	31.5	0.58	0.86	0.681	0.516–0.846	–	0.32	0.10	3.101	1.814–4.387	+	0.10	0.04	2.392	0.313– 4.472	o
1995	19.5	0.45	0.45	0.995	0.644–1.346	o	0.26	0.45	0.575	0.268–0.882	–	0.29	0.10	2.943	1.494– 4.393	+
1996	96.1	0.49	0.56	0.883	0.731–1.035	o	0.28	0.40	0.685	0.500–0.870	–	0.23	0.04	5.742	3.943– 7.540	+
Biomass																
1991	—	0.42	0.53	0.789	0.767–1.811	–	0.15	0.42	0.364	0.343–0.384	–	0.43	0.05	9.069	8.083–10.056	+
1992	—	0.20	0.15	1.315	1.228–1.402	+	0.43	0.69	0.620	0.599–0.642	–	0.37	0.16	2.366	2.209– 2.523	+
1993	—	0.18	0.30	0.586	0.561–0.601	–	0.42	0.41	1.042	1.019–1.065	+	0.40	0.29	1.366	1.316– 1.416	+
1994	—	0.31	0.63	0.494	0.445–0.543	–	0.33	0.14	2.346	2.151–2.540	+	0.36	0.23	1.586	1.396– 1.776	+
1995	—	0.15	0.26	0.596	0.525–0.668	–	0.16	0.37	0.437	0.393–0.481	–	0.68	0.37	1.837	1.721– 1.953	+
1996	—	0.20	0.35	0.574	0.541–0.607	–	0.21	0.47	0.454	0.431–0.477	–	0.58	0.18	3.287	2.988– 3.586	+

[a] Log-likelihood χ^2 test for any form of prey selection during a breeding season. Critical test value given 2 degrees of freedom and alpha = 0.05 is 5.991.
χ^2 test on biomass values (g of prey) was not considered appropriate.

[b] '+' indicates prey taken in greater proportion relative to availability, and hence, selection; 'o' indicates prey taken in same proportion as availability;
'–' indicates prey taken in less proportion than is available, or avoidance.

Table 3.6. Coefficients of modeled effects on reproductive potential (*RP*) of Mexican spotted owls in the Sacramento Mountains, New Mexico (1991–1996) and weights of model reliability. Sample size was 66 owl territories where number of young produced could be adequately determined in ≥1 year. Independent (regressor) variables where averages among years for which reproductive data were available. Model order based on ΔAIC_c. Regressor variables are described further in the text and Table 3.2.

RP[a]		R^2	Original Models[c]		All Models[d]		INTER-	FW-	NST-					
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	CEPT	TEMP	RAIN	NEMEA	PEMAA	PEBOA	MILOA	MIMEA
E8	4	16.7	–	–	0	0.1196*	−16.912	–	–	–	–	–	–	–
E3	4	16.4	–	–	0.22	0.1071*	0.454	–	−0.014	–	–	–	–	–
E1	4	16.3	–	–	0.27	0.1044*	0.446	–	−0.018	–	–	–	–	–
E2	4	16.1	–	–	0.41	0.0976*	0.406	–	−0.018	–	–	–	–	–
C10	5	18.9	0	0.1604*	0.58	0.0896*	0.405	–	−0.019	–	–	–	–	–
C11	5	18.8	0.02	0.1589*	0.60	0.0887*	0.440	–	−0.018	–	–	–	–	–
C21	3	12.2	0.59	0.1194*	1.17	0.0667*	0.346	–	–	–	–	–	–	–
C12	5	17.7	0.95	0.0998*	1.53	0.0556*	0.177	−0.058	−0.028	–	–	–	–	–
C3	6	20.6	1.03	0.0957*	1.61	0.0534*	−0.031	−0.102	−0.026	–	0.0013	0.0043	–	–
C13	5	17.5	1.08	0.0934*	1.66	0.0522*	0.240	−0.522	−0.026	–	–	–	–	–
C5	5	16.8	1.67	0.0694*	2.25	0.0388*	0.333	−0.032	−0.019	–	–	–	–	–
C20	3	10.0	2.26	0.0519*	2.83	0.0290*	0.338	–	–	–	–	–	–	–
C19	3	9.3	2.72	0.0412*	3.30	0.0230*	0.308	–	–	–	–	–	–	–
C16	4	11.2	3.58	0.0268*	4.16	0.0150*	0.512	0.036	–	–	–	–	–	–
C15	4	10.5	4.14	0.0202*	4.72	0.0113*	0.473	0.034	–	–	–	–	–	–
C2	8	22.3	4.64	0.0158*	5.22	0.0088	−0.170	−0.134	−0.043	–	0.0007	0.0066	0.0006	0.0007
C9	4	9.8	4.64	0.0158	5.22	0.0088	0.587	–	−0.013	–	–	–	–	–
E6	4	8.3	–	–	6.29	0.0052	0.537	–	–	–	–	–	–	–
E4	4	7.4	–	–	6.96	0.0037	0.530	–	–	–	–	–	–	–
C7	4	7.3	6.46	0.0064	7.04	0.0036	0.216	−0.099	−0.028	–	–	–	–	–

Table 3.6. (Continued).

RP[a]		R^2	Original Models[c]		All Models[d]		INTER-	FW-	NST-					
Model	K[b]	(%)	ΔAIC_c	Weight	ΔAIC_c	Weight	CEPT	TEMP	RAIN	NEMEA	PEMAA	PEBOA	MILOA	MIMEA
Global	9	23.2	6.63	0.0058	7.21	0.0032	−0.396	−0.128	−0.033	0.0042	0.0017	0.0045	−0.0004	0.0008
C4	6	12.8	7.20	0.0044	7.77	0.0024	0.298	−0.064	−0.033	–	–	–	0.0015	<0.0001
E7	3	2.5	–	–	8.06	0.0021	0.642	–	−0.011	–	–	–	–	–
E5	4	5.5	–	–	8.27	0.0019	0.536	–	–	–	–	–	–	–
C22	3	2.1	7.76	0.0033	8.34	0.0018	0.415	–	–	–	–	–	–	–
C14	5	8.0	8.28	0.0026	8.86	0.0014	0.075	−0.118	−0.032	–	–	–	–	–
C1	5	7.8	8.45	0.0023	9.03	0.0013	0.385	−0.078	−0.023	−0.0020	–	–	–	–
C6	5	7.4	8.70	0.0021	9.28	0.0012	0.231	−0.086	−0.026	–	–	–	–	–
C23	3	0.2	9.08	0.0017	9.66	0.0010	0.574	–	–	–	–	–	–	–
C17	4	2.4	9.84	0.0012	10.42	0.0006	0.492	0.017	–	–	–	–	–	–
C8	4	1.6	10.39	0.0009	10.97	0.0005	0.411	0.021	–	–	–	–	–	–
C18	4	0.2	11.34	0.0006	11.92	0.0003	0.551	−0.004	–	–	–	–	–	–

Table 3.6. (Continued).

RP[a] Model	PFS-RAIN	ENT-TEMP	COMPA	SMLPA	MF-PREY	MFHA	HABEV	SNST-RAIN	SCO-MPA	SSM-LPA	SMF-PREY	ELEV	ELEV^2
E8	–	–	–	–	–	–	–	–	–	–	–	0.0135	<0.0001
E3	–	–	–	–	0.0008	–	–	–	–	–	–	–	–
E1	–	–	–	0.0008	–	–	–	–	–	–	–	–	–
E2	–	–	0.0008	–	–	–	–	–	–	–	–	–	–
C10	–	−0.0466	0.0007	–	–	–	–	–	–	–	–	–	–
C11	–	−0.0451	–	0.0007	–	–	–	–	–	–	–	–	–
C21	–	–	–	–	0.0008	–	–	–	–	–	–	–	–
C12	–	–	0.0008	–	–	–	–	–	–	–	–	–	–
C3	–	–	–	–	–	–	–	–	–	–	–	–	–
C13	–	–	–	0.0007	–	–	–	–	–	–	–	–	–
C5	–	–	–	–	0.0008	–	–	–	–	–	–	–	–
C20	–	–	–	0.0007	–	–	–	–	–	–	–	–	–
C19	–	–	0.0007	–	–	–	–	–	–	–	–	–	–
C16	–	–	–	0.0008	–	–	–	–	–	–	–	–	–
C15	–	–	0.0008	–	–	–	–	–	–	–	–	–	–
C2	–	–	–	–	–	–	–	–	–	–	–	–	–
C9	–	−0.0725	–	–	–	–	–	–	–	–	–	–	–
E6	–	–	–	–	–	–	–	−0.0068	–	–	0.2432	–	–
E4	–	–	–	–	–	–	–	−0.0070	–	0.2174	–	–	–
C7	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 3.6. (Continued).

RP[a] Model	PFS-RAIN	ENT-TEMP	COMPA	SMLPA	MF-PREY	MFHA	HABEV	SNST-RAIN	SCO-MPA	SSM-LPA	SMF-PREY	ELEV	ELEV^2
Global	–	–	–	–	–	–	–	–	–	–	–	–	–
C4	–	–	–	–	–	–	–	–	–	–	–	–	–
E7	–	–	–	–	–	–	–	–	–	–	–	–	–
E5	–	–	–	–	–	–	–	−0.0066	0.1722	–	–	–	–
C22	–	–	–	–	–	0.0004	–	–	–	–	–	–	–
C14	–	–	–	–	–	–	0.1612	–	–	–	–	–	–
C1	–	–	–	–	–	–	–	–	–	–	–	–	–
C6	–	–	–	–	–	0.0001	–	–	–	–	–	–	–
C23	–	–	–	–	–	–	−0.0656	–	–	–	–	–	–
C17	–	–	–	–	–	0.0005	–	–	–	–	–	–	–
C8	0.0071	–	–	–	–	–	–	–	–	–	–	–	–
C18	–	–	–	–	–	–	−0.0614	–	–	–	–	–	–

[a] Linear regression models of spotted owl reproductive potential described in Table 3.2.

[b] Number of model parameters estimated from data including intercept coefficient, effect coefficients, and a residual error term.

[c] Weighted according to minimum AIC_c value of the 24 *a priori* models.

[d] Weighted according to minimum AIC_c value of the 24 *a priori* and eight exploratory models.

Table 3.7. Precision and relative importance of ecological factors associated with reproductive potential of Mexican spotted owls in the Sacramento Mountains, New Mexico (1991–1996). Two sets of regression coefficients (β) are given; those averaged over *a priori* (original) models and the other averaged over original and exploratory (all) models. CVs of the average coefficients include variation associated with uncertainty of model structure. Relative importance (RI) of each factor is also shown for both model sets and is based on the sums of Akaike weights for each model that included the factor. Asterisks indicate effects included in the 95% confidence set of models. Factor acronyms are defined in the text. Factors are ordered from highest to lowest according to RI in the original model set.

	Original Models			All Models		
Factor	$\overline{\beta}$	CV(%)	RI	$\overline{\beta}$	CV(%)	RI
NSTRAIN	−0.01652	59.7	0.733*	−0.01440	59.5	0.720*
FWTEMP	−0.02533	136.3	0.447*	−0.01414	144.1	0.250*
ENTEMP	−0.01578	96.0	0.335*	−0.00881	106.7	0.187*
SMLPA	0.00023	76.5	0.331*	0.00022	79.2	0.289*
COMPA	0.00023	77.4	0.322*	0.00021	80.4	0.277*
MFPREY	0.00014	88.4	0.189*	0.00017	85.4	0.213*
PEMAA	0.00014	105.1	0.117*	0.00008	109.5	0.066*
PEBOA	0.00054	116.5	0.117*	0.00030	120.5	0.066*
MILOA	0.00001	307.7	0.026*	0.00001	308.0	0.015
MIMEA	0.00002	182.6	0.026*	0.00001	183.2	0.015
NEMEA	0.00002	247.0	0.008	0.00001	247.1	0.005
MFHA	<0.00001	156.1	0.007	<0.00001	156.3	0.004
HABEV	0.00027	457.6	0.005	0.00015	457.6	0.003
PFSRAIN	0.00001	141.5	0.001	<0.00001	141.5	0
SNSTRAIN	–	–	–	−0.00007	110.2	0.004
SCOMPA	–	–	–	0.00033	114.1	0.002
SSMLPA	–	–	–	0.00080	110.0	0.004
SMFPREY	–	–	–	0.00125	108.6	0.005
ELEV	–	–	–	0.00162	524.5	0.120*
$ELEV^2$	–	–	–	<0.00001	37,813.2	0.120*

Table 3.8. Relationships between annual reproductive output by Mexican spotted owls in the Sacramento Mountains, New Mexico (1991–1996) and selected environmental variables describing summer biomass (kg) of common prey species, habitat amounts, or weather. Sample size is 6 breeding seasons for each correlation. Asterisks indicate strong evidence for covariation ($P < 0.10$).

Environmental Variable	Correlation Coefficient (r)	Statistical Probability (P)
Deer mouse biomass (kg)	0.64	0.173
Brush mouse biomass (kg)	0.37	0.468
Mexican vole biomass (kg)	0.53	0.277
Long-tailed vole biomass (kg)	0.68	0.135
Mexican woodrat biomass (kg)	−0.01	0.981
Mouse and vole biomass (kg)	0.78	0.070*
Five common prey biomass (kg)	0.78	0.060*
Common prey biomass (kg) in mesic forest	0.76	0.082*
Common prey biomass (kg) in meadows	0.54	0.270
Common prey biomass (kg) in xeric forest	0.41	0.418
Amount of mesic forest (ha)	−0.20	0.709
Amount of meadow (ha)	0.27	0.602
Amount of xeric forest (ha)	<0.01	1.000
Amount of mesic forest and meadow (ha)	−0.17	0.747
Mean minimum temperature during fall–winter (°C)	0.21	0.691
Minimum temperature during early nesting (°C)	0.44	0.388
Amount of precipitation during fall–spring (cm)	−0.14	0.786
Amount of precipitation during nesting period (cm)	−0.15	0.777

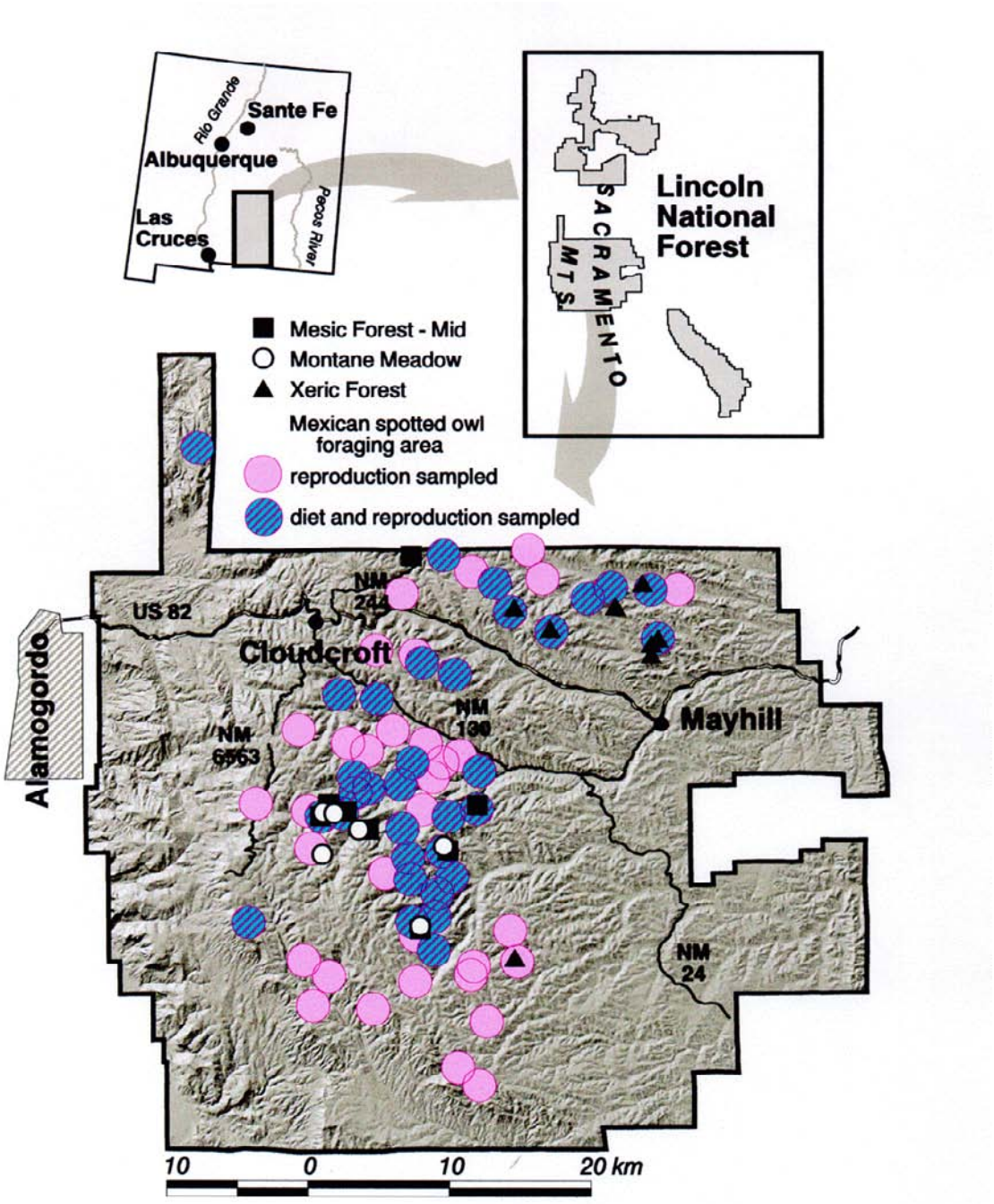

Figure 3.1. Distribution of Mexican spotted owl territories from which diet samples were collected and number of young owls recorded, and location of sites where prey populations were sampled in the Sacramento Mountains, New Mexico (1991–1996). Mesic-forest sites were in a mid-seral (M) stage whereby most trees were 60-100 years in age. Owl territory symbols are shown to scale and equal the size of foraging areas during the breeding season (467 ha). Prey-sampling sites are greatly enlarged for presentation.

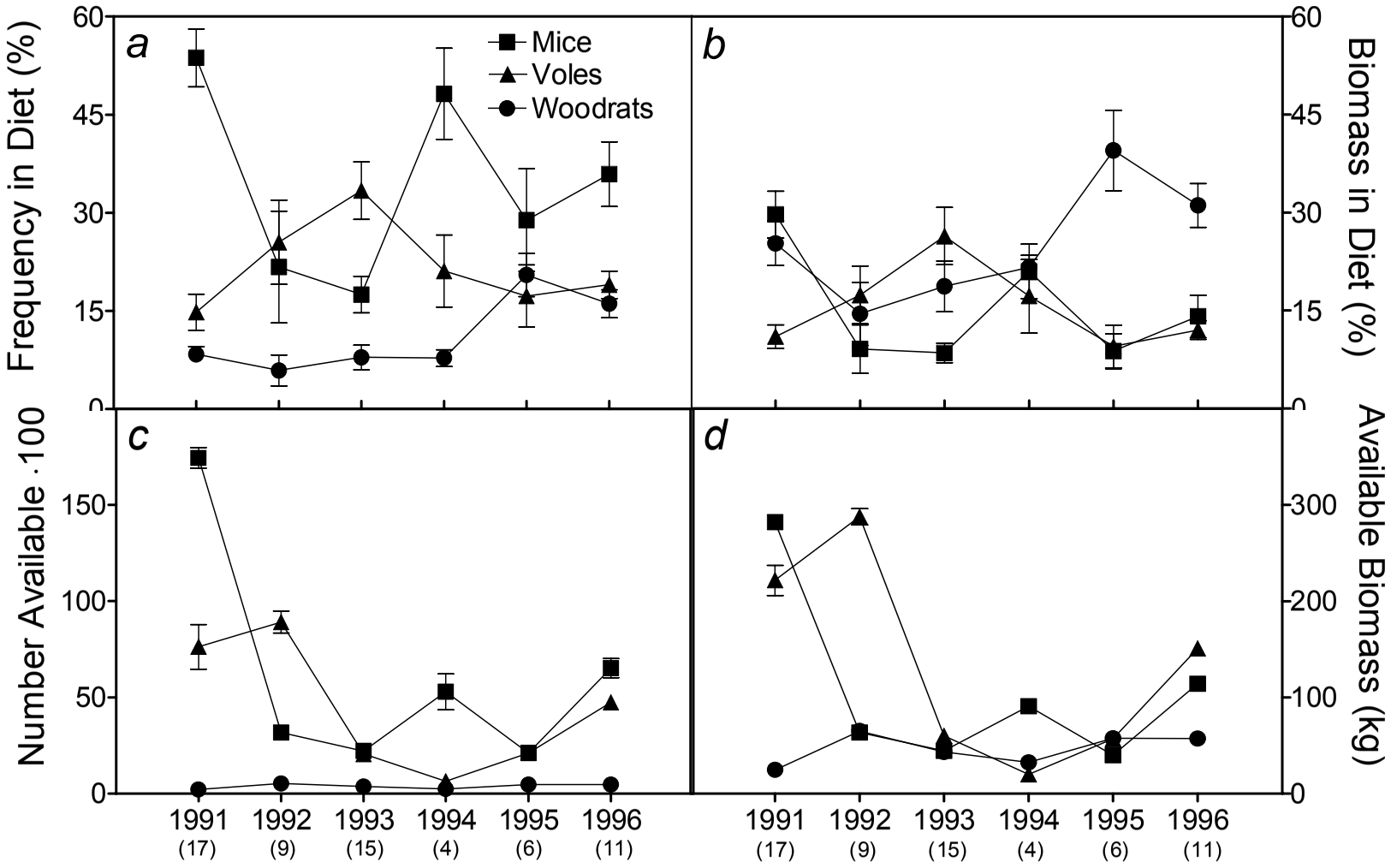

Figure 3.2. Relative frequency (*a*) and percent biomass (*b*) of three common prey genera consumed by Mexican spotted owls in the Sacramento Mountains, New Mexico during six breeding seasons (1991–1996) and amount of these prey available *c* and *d*). Standard errors are shown for dietary measures and 95% confidence intervals are shown for estimates of prey availability.

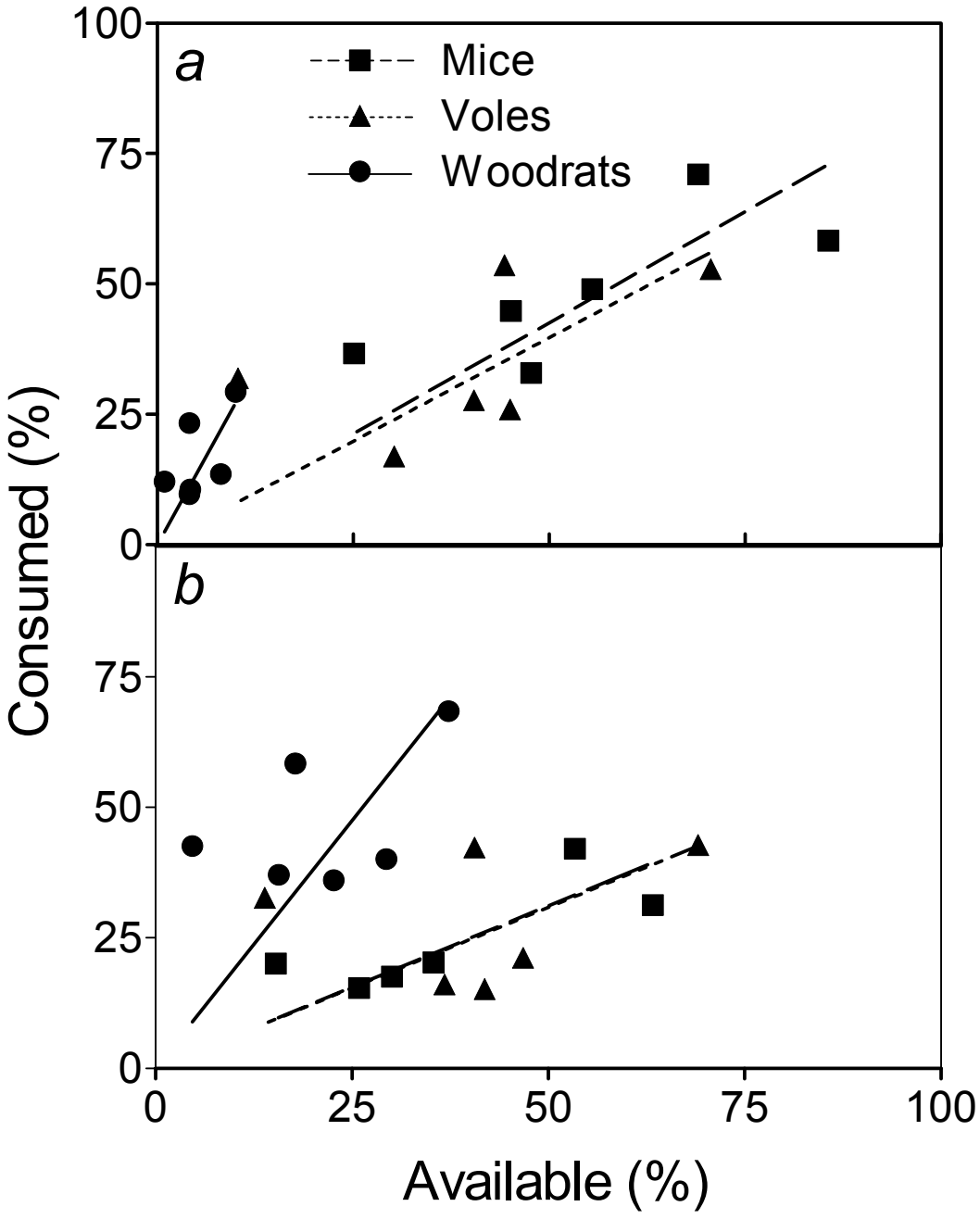

Figure 3.3. Relative functional response by Mexican spotted owls in the Sacramento Mountains, New Mexico. Examination of relative frequency (*a*) or percent biomass (*b*), indicated that woodrats (*Neotoma* spp.) were selected and elicited a significantly stronger response (slope >1) compared to mice and voles (*Peromyscus* spp., *Microtus* spp.) which on average were taken in accordance with their abundance (slope = 1) during six breeding seasons (1991–1996). All regressions were conducted on arcsine-square root transformations and were statistically significant ($\alpha = 0.05$).

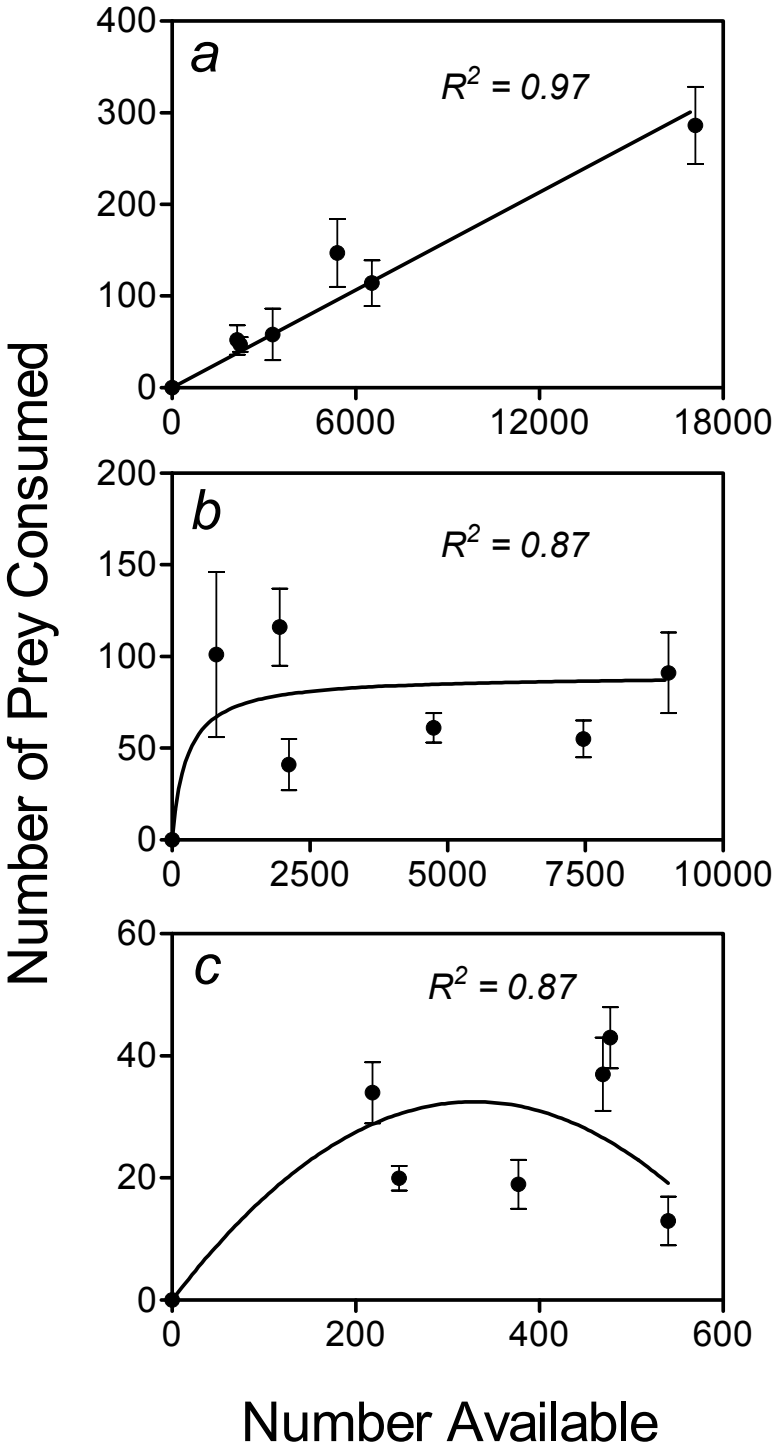

Figure 3.4. Absolute functional responses of Mexican spotted owls to (*a*) mice (*Peromyscus* spp.), (b) voles (*Microtus* spp.), and (c) woodrats (*Neotoma* spp.) occurring in the Sacramento Mountains, New Mexico during six breeding seasons (1991–1996). Error bars are SE. Please note the different scales in each graph.

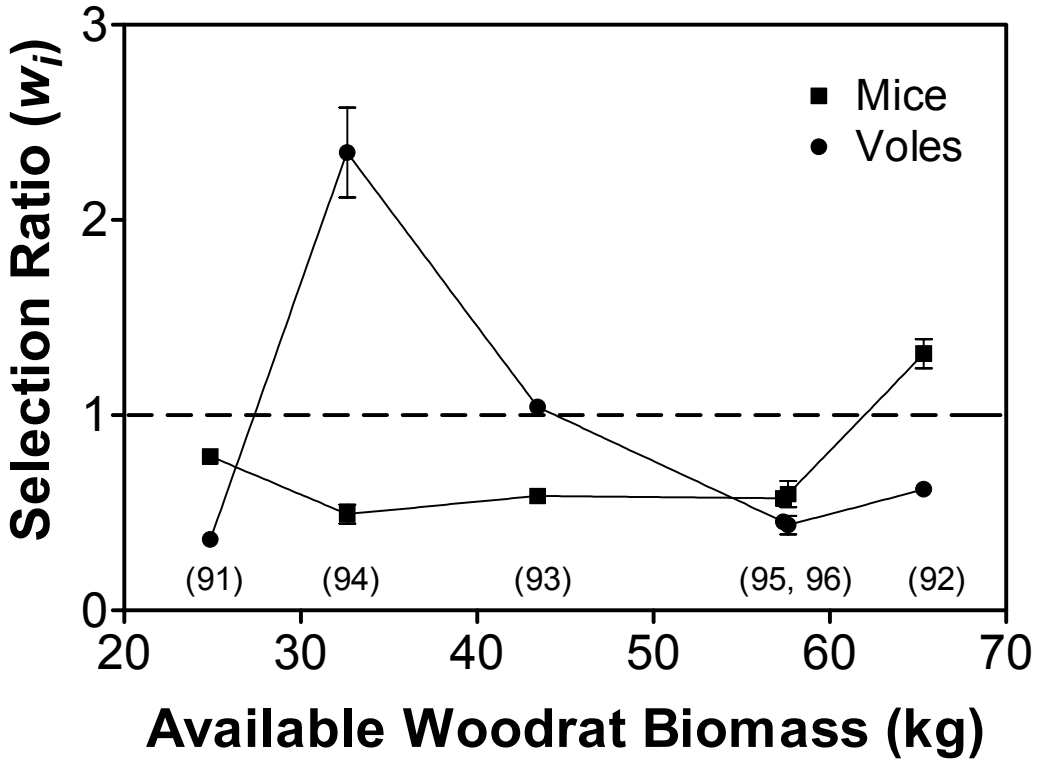

Figure 3.5. Selection of alternative prey (mice [*Permomyscus* spp.] and voles [*Microtus* spp.]) by Mexican spotted owls occurring in the Sacramento Mountains, New Mexico during six breeding seasons (1991–1996) as a function of availability of primary prey (woodrat [*Neotoma* spp.]) biomass. Error bars are 95% CI. Selection ratios (w_i) > 1.0 indicate positive selection for that prey. Switching occurs when alternative prey are selected while primary prey are less available, as shown here for voles but not mice. Year of each breeding season is referenced in parentheses.

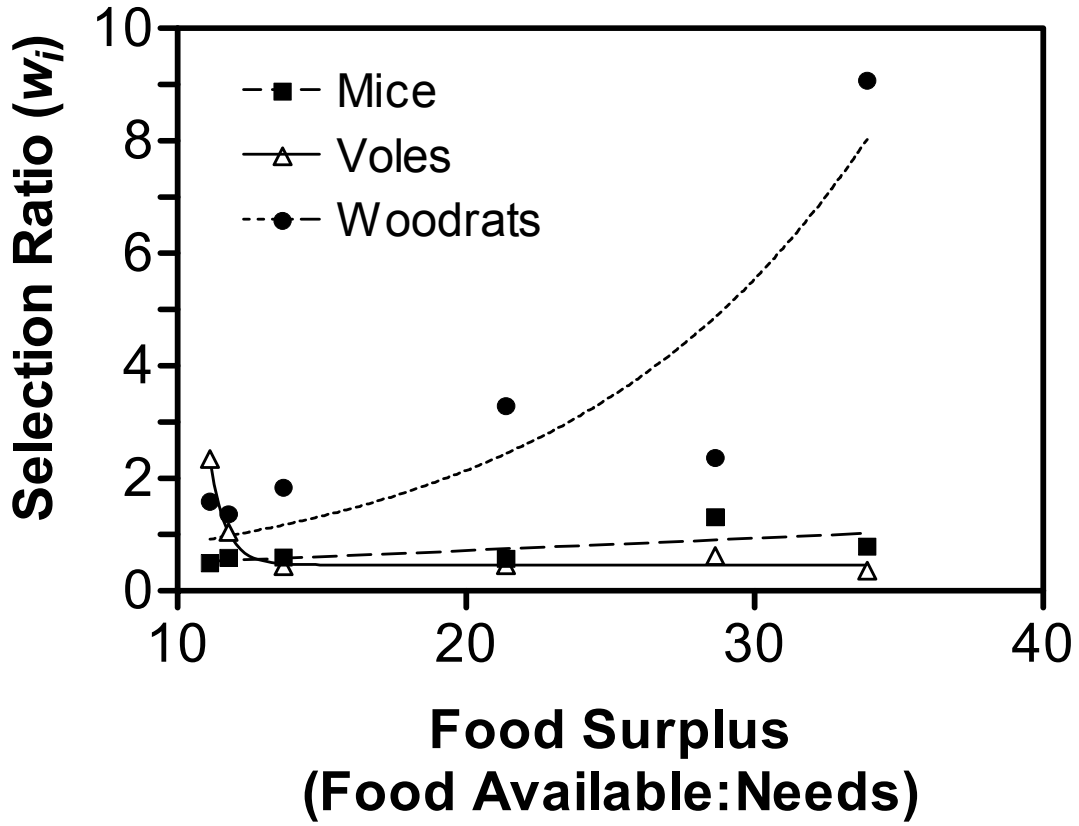

Figure 3.6. Prey preferences by Mexican spotted owls in the Sacramento Mountains, New Mexico during six consecutive breeding seasons (1991–1996). Selection ratios >1 indicate that prey were taken greater than expected given their availability. Woodrats (*Neotoma* spp.) appeared to be preferred because selection for this prey increases disproportionately when food is abundant relative to the owl's needs.

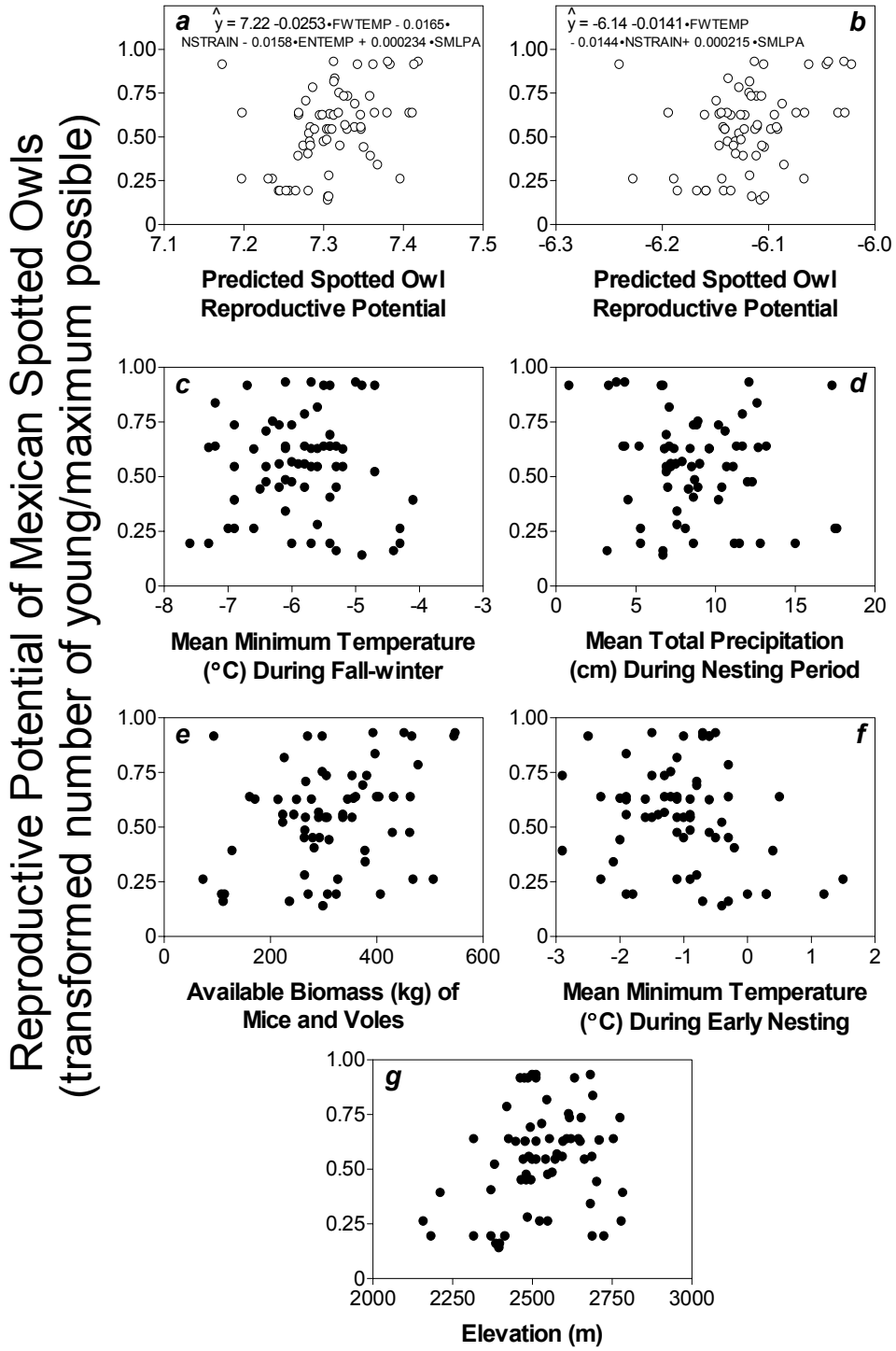

Figure 3.7. Reproductive potential of Mexican spotted owls in the Sacramento Mountains, New Mexico, and (*a*) reproductive potential predicted by top ranked factors from original models, or (*b*) predicted by top ranked factors from original and exploratory models. Coefficients in predictive models are model-averaged values. Also shown are relationships with each factor included in the models (*c–f*) and with (*g*) elevation.

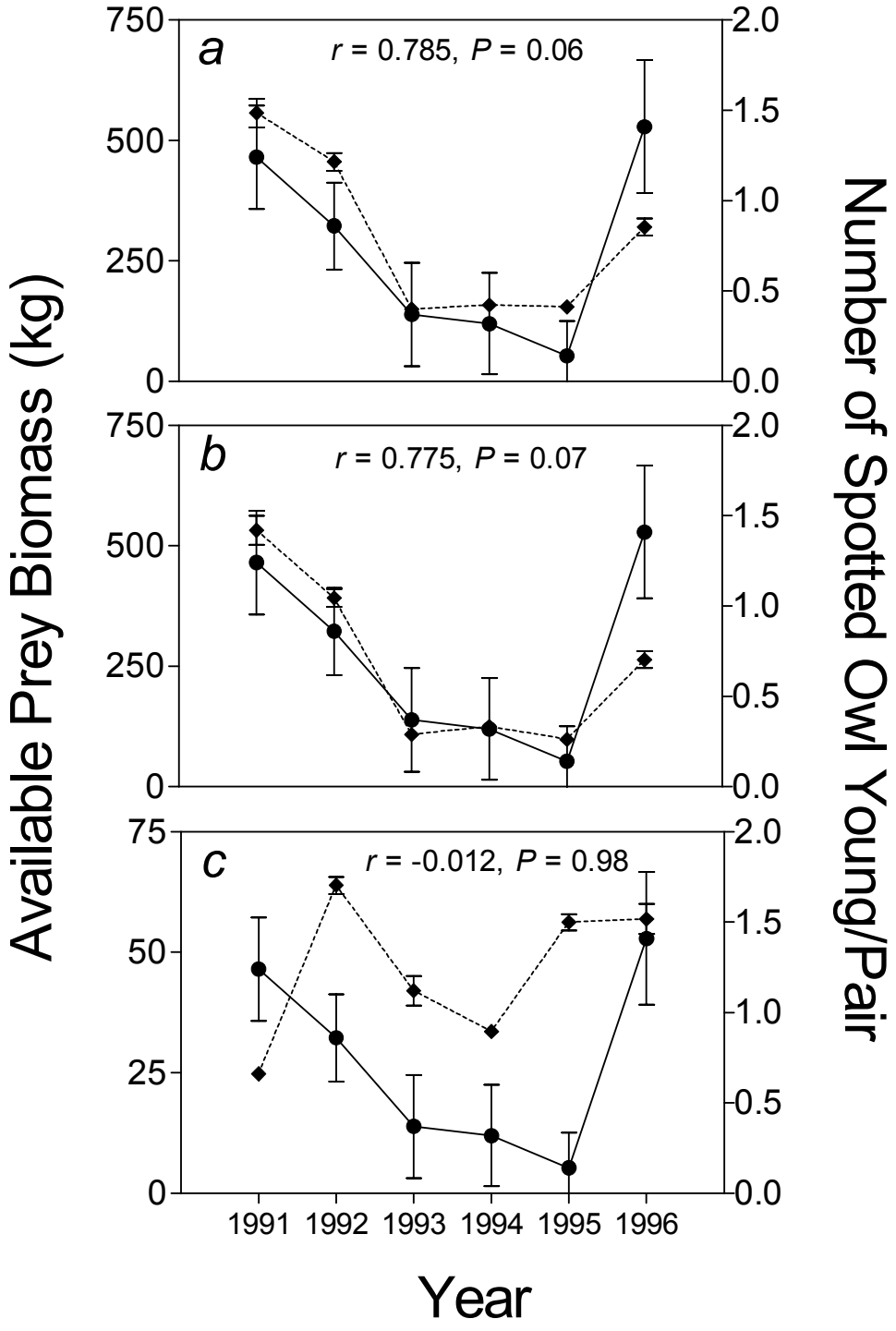

Figure 3.8. Relationship between annual reproductive output by Mexican spotted owls and available biomass of (*a*) five common prey species, (*b*) mice and voles, and (*c*) Mexican woodrats in the Sacramento Mountains, New Mexico (1991–1996).

APPENDIX 3.A
Definition of Prey Availability

Prey availability imparts both the abundance and accessability of prey to a predator. Whereas abundance is conceptually succinct and its measurement well documented (Seber 1982, White et al. 1982, Krebs 1989), protocols for defining and measuring accessability are not well established (Hutto 1990). The manner in which availability is defined can influence inferences about prey selection (Johnson 1980, Aebischer et al. 1993, Manly et al. 1993). It is therefore important for investigators to describe what their measures of availability represent when quantifying resource selection (Hutto 1990, Hall et al. 1997). That is the purpose of this appendix.

Conceivably, the number of prey that can be accessed by a predator during a specified time frame comprises some portion of absolute abundance that is determined by factors that limit predation (Fig. 3A.1). For example, when prey availability is set equal to prey abundance without considering predation limits, it is implied that all prey individuals occupying the space associated with that abundance can be accessed by the focal predator. This occurs when an investigator substitutes prey abundance estimated for a generalized study area because the only (and artificial) constraint on prey availability is the spatial extent of the study area and the sampling design. Unfortunately, ignoring limits to predator access may overstate or produce biologically unrealistic measures of prey availability, which in turn, influence the evaluation of prey selection (Johnson 1980, Aebischer et al. 1993).

A number of ecological factors may impact a predator's access to prey depending upon the process of predation. For example, three events must transpire for predation to succeed, (1) predator and prey must co-occur, (2) the predator must detect its prey, and (3) detected prey cannot evade capture (i.e., the prey must be vulnerable to capture). Co-occurrence of predator and prey is predicated on mutual use of space determined by habitat choice and movement by the interacting species. Detection and subsequent capture of prey by the predator (or detection and avoidance of predator by the prey) may be influenced by habitat structure, weather, morphology, and behavior of the interacting organisms (Southern and Lowe 1968, Clarke 1983, Janes 1985, Kolter 1985, Martin 1986, Temple 1987, Kolter et al. 1988, Derting and Cranford 1989, Hutto 1990, Martínez and Jaksić 1997, Sakai and Noon 1997; Fig. 3A.1).

Considering the process of predation in this manner also helps to identify the appropriate spatial and temporal scales for assessing prey availability (Wiens et al. 1986). For example, the quantity of geographic space associated with the three events of predation can be seen as a hierarchical scale for nonsessile species (Johnson 1980; Fig. 3A.1). The area associated with traveling and searching for prey will naturally be larger than the area over which prey can be detected, which in turn, will be larger in extent than the specific locality where prey are seized. The extent of area over which prey are accessed, and hence availability should be measured, is also coupled with time. For most predators, the culmination of a single predation event occurs quickly at a solitary locality. However, additional time is usually expended and additional area usually searched by a predator prior to capturing prey. Likewise, over an extended period of time, the associated aggregation of predation events can constitute a larger geographic space. Accordingly, the appropriate availability measure should encompass the temporal and spatial dimensions of the factors that limit a predator's access to its prey.

Following this reasoning, I define two general levels at which availability can be measured (Fig 3A.1). One pertains to the area over which a predator searches for prey during a specified time period. The other is the area over which prey detection occurs. Both levels are influenced by different ecological factors and both are associated with different spatial extent. Availability measured at the first level considers accessability by limiting prey abundance to that area actually searched by the predator. Availability measured at the second level mimics further constraints on access by limiting the number of prey considered available to that area where prey can be detected (Hutto 1990). In this fashion, availability of prey over longer periods can be represented by the abundance of prey that occurred within the sum of areas defined by either the predator's foraging extent (coarse level) or by the predator's ability to detect prey (fine level).

Prey selection quantified as a ratio of relative prey consumption to relative availability is sensitive to availability measures (Aebischer et al. 1993, Manly et al. 1993). Availability measured under coarse-level conditions will be larger than those under fine-level conditions when certain prey species occurring in the area searched by a predator are not detected during a particular foraging period. A larger availability value produces a more conservative selection ratio. Thus, coarse availability measures will indicate significant selection less frequently than fine availability measures for those species that are hard to detect. Relative to coarse-level measures of availability, fine level measures require more detailed information on detection rates, that are influenced by behavioral reactions and morphological features associated with predation and predator avoidance; information that is usually lacking and that entails well defined experiments (Hutto 1990). In this study, I quantified prey availability at the coarse level.

Mathematically, coarse availability of prey *i* would be estimated as,

$$Availability_i = \sum_{j=1}^{H=3} (\hat{D}_{ij} \cdot \hat{h}_j) \qquad (3.A.1)$$

where $\hat{D}_{ij}$ is the density of prey *i* in habitat *j* and $\hat{h}_j$ is the amount of area of habitat *j* hunted by Mexican spotted owls during a specified period. Arguably, the availability of prey in certain habitats will be affected further if owls exercise a preference for habitat type when foraging. In this case, coarse availability of prey can be estimated as,

$$Availability_i = \sum_{j=1}^{H=3} (\hat{D}_{ij} \cdot \hat{h}_j \cdot \hat{B}_j) \qquad (3.A.2)$$

where $\hat{B}_j$ is a standardized habitat selection function (Manly et al. 1993:40). Sampling variance for either availability parameter can be estimated from the products of sampling variances associated with each parameter on the right hand side of the equations following Goodman (1960). Use of equation 3.A.2 requires information on the frequency of use and availability of each foraging habitat. A similar approach was used by Greenlaw and Post (1995) to identify prey selection by seaside sparrows (*Ammodramus maritimus*). Although, Mexican spotted owls likely prefer certain habitats when foraging, I estimated the amount of prey available to these owls using equation 3.A.1 because existing data on foraging habitat selection were imprecise Ganey et. al. (*in review*).

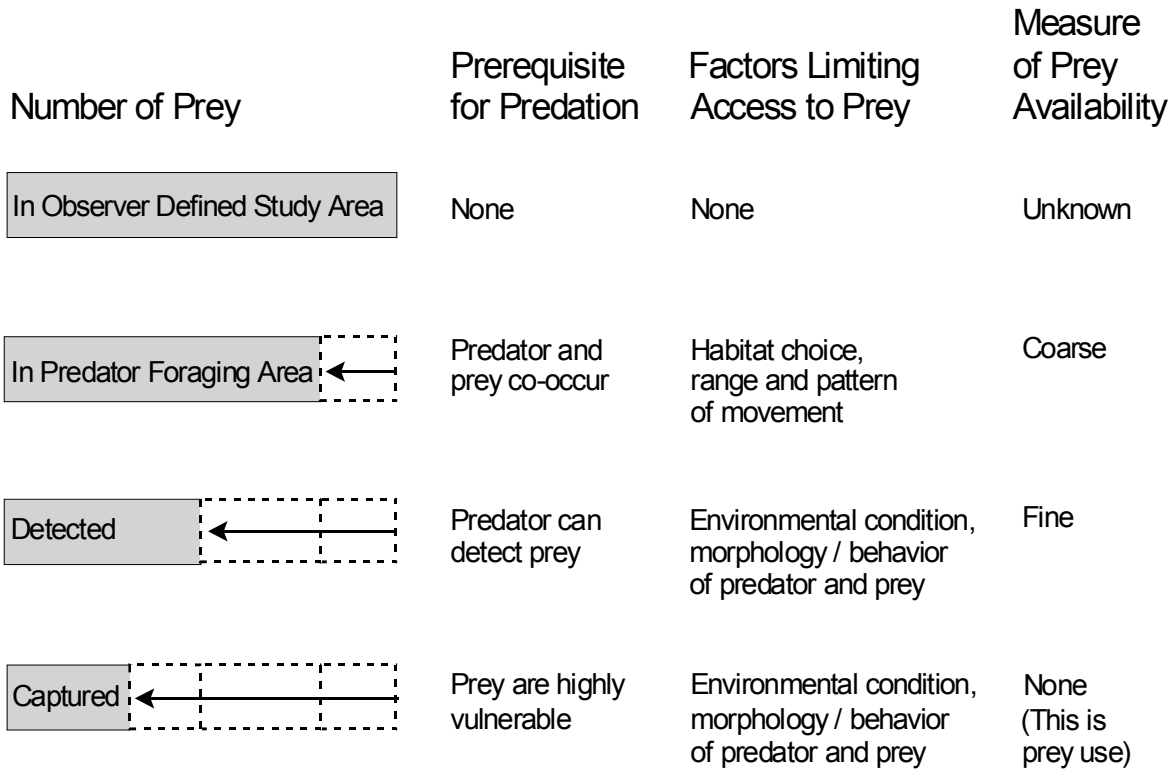

Figure 3A.1. Conceptualization of prey availability as a function of prey abundance and a predator's access to its prey during a specified time period. Several ecological factors can limit a predator's access to its prey but these vary according to the process of predation. Consequently, the abundance of prey may connote different measures of availability depending on the level at which it is measured. In this study, availability of prey common to Mexican spotted owls was measured at the coarse level.

APPENDIX 3.B
Estimation of Mexican Spotted Owl Foraging Areas

In this study, amount of prey available to Mexican spotted owls was estimated from habitat-specific densities of prey ($\hat{N}$/ha) and amounts of those habitats (ha) available to spotted owls for hunting. The latter were calculated as areas occurring within 467-ha circles, which were deemed representative of foraging areas of male spotted owls during the breeding season in the Sacramento Mountains, New Mexico. The purpose of this appendix is to explain how that size of foraging area was determined, and why the composition of the circular areas was considered representative of foraging habitat available to the owl.

I estimated foraging areas of male spotted owls using conventional analysis of radio-telemetry data (White and Garrot 1990). These data were collected during a habitat-use study conducted from 1992 to 1994 by J. L. Ganey, Rocky Mountain Research Station (Ganey et al., *in review*). I determined an average-sized foraging range by estimating the average minimum convex polygon (MCP; Mohr 1947) area that included all nighttime locations of eight radio-marked spotted owls during the breeding season (1 Mar to 31 Aug) of 1993. All locations were estimated from ≥ 3 telemetry vectors that created a polygon ≥ 2 ha in size. Accuracy of nighttime locations was unknown. However, daytime telemetry (estimated) locations were found to be 178 m on average from (true) locations of owls observed at their roosts (SE = 75.5 m; n = 8 owls with an average of 48 double sampled locations/owl).

I used program CALHOME to estimate MCP areas for each owl sampled (Kie et al. 1996). The average MCP was 467 ha (SE = 86.1ha; n = 8 male owls) based on an average of 90 locations per owl (SE = 7.1). The sample of locations and duration appeared sufficient given reported effects of sample size on home range estimators (Ganey et al., *in review*; Seamen et al. 1999).

I used the MCP method because it is most commonly used and I considered it the most satisfactory for estimating an area that was available for hunting. However, the MCP estimator has been considered less efficient because it can include large areas never used by monitored individuals (White and Garrot 1990). Unfortunately, it is difficult to determine if areas not used within the organism's range of mobility were also not available. Recent studies have found the adaptive kernel method (ADK) to be a more

reliable estimator of home-range size and shape (Worton 1989, Boulanger and White 1990). However, ADK is based on distributions of use locations and foraging ranges estimated from this method could greatly underestimate available but unused amounts of habitat. To gauge the potential for exaggerating amounts of available habitat with the MCP method, I estimated average foraging range size from the same set of nighttime locations using the ADK method, which is also offered in program CALHOME. The ADK estimates were based on 95% contour and cell size determined automatically during the course of analysis (Kie et al. 1996). I found that the average size of male foraging ranges were surprisingly close for both methods (MCP: $\bar{x}$ = 467, SE = 86.1 ha; ADK: $\bar{x}$ = 450, SE = 82.7 ha; n = 8 owls). I therefore considered the average MCP estimate a reasonable size for estimating available foraging habitat.

To extrapolate circular foraging areas to the individual owls for which food habits were studied, I would have to assume that (1) composition of available habitat was accurately represented within the circular areas, and (2) radio-telemetry data gathered from a sample of owls during one breeding season was representative for the population during 2 prior breeding seasons preceding and 3 subsequent breeding seasons.

To evaluate the composition of the circular foraging areas, I tested the statistical hypothesis that proportions of mesic forest-mid seral stage (MF), montane meadow (MM), and xeric forest (XF) were not different among three configurations of foraging range (circles, MCP, ADK) estimated for the same eight male spotted owls (Table 3.B.1). I used a multiple response permutation procedure while blocking on each individual owl (MRBP; Slauson et al. 1991) to calculate an exact probability that the proportions of available habitat within each configuration were from the same distribution (Edgington, 1987). I found that the habitat proportions were very similar among the three foraging-range configurations (P = 0.908).

The sample of eight radio-marked owls was not selected at random from the Sacramento Mountain owl population. However, the areas occupied by the sampled individuals spanned the range of ecological conditions occupied by the population. Size and configuration of home ranges and feeding territories are affected by a number factors including habitat condition, amounts and types of prey, and density of conspecifics (Schoener 1968, Carey et al. 1992, Zabel et al. 1995). These factors varied considerably for the sample of spotted owls examined and likely reflected the range of conditions experienced by the majority of this population (Ganey et al., *in review*). I therefore considered this sample of foraging areas representative for the entire population.

Arguably, estimates of foraging ranges from one breeding season (1993) may not represent those in other years, particularly when ecological conditions that influence the owls foraging patterns change with time. Limits on telemetry data prevented me from

evaluating this assumption. Although I maintained a constant size (467 ha) and configuration of the foraging area for all owls in all years, I did allow for the location of the foraging area to shift through time according to shifts in each owl's center of activity among breeding seasons. Shifts of the center point of a circular area could result in different proportions of habitat being included in the foraging area over time. Given all of the above considerations, I assumed that the 467-ha circular areas were reasonable approximations of male spotted owl foraging areas for the purpose of estimating available foraging habitat. Annual average amounts of each habitat (ha) estimated across foraging ranges from which the owl's food habits were known varied slightly among years (Table 3.B.2).

Table 3.B.1. Proportions of foraging habitat available to male Mexican spotted owls during the breeding season (1993) in the Sacramento Mountains, New Mexico, given three configurations of the owl's foraging range.

	Mesic Forest-M(%)			Xeric Forest (%)			Meadow (%)		
Owl	CIR[a]	MCP	ADK	CIR	MCP	ADK	CIR	MCP	ADK
4	54.2	56.6	56.5	36.7	30.2	38.6	2.1	3.1	1.5
7	85.0	87.2	85.2	7.8	9.7	5.7	4.2	3.1	3.0
17	49.3	47.8	49.3	47.4	42.0	43.8	3.3	10.2	6.9
24	66.0	63.9	69.9	8.8	10.4	9.2	7.7	5.5	5.1
26	89.0	96.0	67.7	3.7	0	7.2	4.5	0.2	5.4
47	78.3	91.1	78.3	3.2	0	6.7	6.9	6.8	5.1
72	21.1	29.5	27.5	55.3	46.2	57.0	2.0	0.1	0
77	52.0	60.6	46.0	47.2	38.3	52.9	0.8	1.1	1.1

[a] CIR = circle ($\bar{x}$ = 467 ha); MCP = minimum convex polygon ($\bar{x}$ = 467 ha); ADK = adaptive kernel 95% ($\bar{x}$ = 450 ha).

Table 3.B.2. Mean amounts of habitats (ha) in 467-ha foraging ranges of male Mexican spotted owls occurring in the Sacramento Mountains, New Mexico (1991–1996). Estimates were made using digital coverages classified to forest type (USDA Forest Service, Lincoln National Forest, *unpublished data*).

Year	Mesic Forest $\bar{x}$	(SE)	Meadow $\bar{x}$	(SE)	Xeric Forest $\bar{x}$	(SE)	Other $\bar{x}$	(SE)	Number of Owl Ranges
1991	316.3	(26.70)	22.5	(3.16)	93.7	(30.30)	34.3	(7.91)	17
1992	334.4	(24.05)	17.0	(3.40)	85.2	(26.24)	30.1	(7.75)	9
1993	294.8	(27.17)	21.7	(4.33)	118.8	(29.98)	31.4	(7.72)	15
1994	318.0	(59.04)	15.3	(5.43)	83.8	(55.44)	49.7	(14.45)	4
1995	318.4	(50.70)	23.5	(6.30)	112.1	(53.86)	12.7	(3.09)	6
1996	345.0	(17.46)	26.5	(4.05)	65.3	(17.08)	29.9	(7.62)	11

APPENDIX 3.C
Estimation of Weather Parameters

During development of *a priori* models, several weather variables were identified as key factors that could influence reproduction by Mexican spotted owls. These variables included, cumulative rainfall (cm) during the nesting period (March–May) (NSTRAIN), cumulative rainfall during a previous fall through to the spring (September–April) immediately preceding raising of young (PFSRAIN), average minimum temperatures (°C) during late fall and winter months (November–February) prior to a given breeding season (FWTEMP), and mean minimum temperature during early nesting (April; ENTEMP). The modeling approach used in this study required site- and time- specific observations for these variables. Although precipitation categories and minimum and maximum temperatures were recorded at each grid during periods of small-mammal trapping, these data were not sufficient. Rather, I input expected weather values given the elevation (m) of each site (taken at a spotted owl roost or nest center of each territory during a given year) and a predictive equation. In this appendix, I describe the procedures used to estimate the expected weather values.

I developed the predictive equations retrospectively from data recorded at nine weather stations (Table 3.C.1). I modeled the relationship between each weather variable and elevation of the weather station using simple linear regression. I used the least squares method to estimate intercept and slope coefficients (Table 3.C.2). All relationships were statistically significant (P of all F-tests ranged 0.0001–0.03) except for the relationship of NSTRAIN in 1994 and 1996 ($P = 0.14$). Excepting these two cases, the amount of variation explained by each significant relationship was moderately high (R^2 ranged 0.53–0.92). Coefficients of variation for slope parameters ranged 11 to 37% (Table 2.A.2). Despite the moderate level of precision, I considered the expected weather values sufficient because these values would be used to identify relative importance among key factors rather than predicting precise estimates of the owl's reproductive potential. I also assumed that estimation of unconditional variances for parameters of the empirical models would be large enough to account for variation associated with estimating the weather variables. Unconditional variance includes uncertainty associated with variation in model structure that can result when different data are analyzed in addition to variation associated with model parameter estimates (Burnham and Anderson 1998).

APPENDIX 3.C (Continued).

Table 3.C.1. Weather stations from which data were compiled and analyzed to estimate expected precipitation and temperature values given elevations in the Sacramento Mountains, New Mexico.

Name	Number [a]	LAT	LONG [b]	Elevation (m)
Alamogordo	290199	32 53	105 57	1326
Tularosa	299165	33 05	106 03	1351
Picacho 2 WSW	296804	33 21	105 10	1537
Carizozo	291515	33 39	105 53	1652
Elk 2	292865	32 57	105 18	1747
Capitan	291440	33 33	105 34	1976
Mountain Park	295960	32 57	105 51	2070
Cloudcroft 2	291931	32 57	105 44	2640
Sunspot Observatory	–	32 47	105 49	2798

[a] National Oceanic and Atmospheric Administration, Cooperative Station number.

[b] Latitude and longitude given as degrees and minutes.

APPENDIX 3.C (Continued).

Table 3.C.2. Coefficients and statistics describing fit of simple linear models used to predict selected weather values from elevation (m) in the Sacramento Mountains, New Mexico. Model form is $Y = \beta_0 + \beta_1 \cdot$ elevation.

Dependent Variable [a]	Year	*n*	β_0	β_1	CV[β_1] (%)	*P* of > *F*-test[c]	R^2
NSTRAIN	1991	9	−5.511	0.0049	30.8	0.015	0.60
NSTRAIN	1992	9	7.134	0.0041	35.4	0.026	0.53
NSTRAIN	1993	9	−2.214	0.0035	36.0	0.027	0.53
NSTRAIN	1994	9	3.029	0.0033	59.0	0.140 ns	0.28
NSTRAIN	1995	9	−1.491	0.0019	26.8	0.007	0.66
NSTRAIN	1996	9	−0.226	0.0004	57.5	0.145 ns	0.28
PFSRAIN	1991	9	−18.428	0.0234	19.0	0.001	0.80
PFSRAIN	1992	9	5.039	0.0153	28.5	0.010	0.64
PFSRAIN	1993	9	−14.924	0.0192	14.6	<0.001	0.87
PFSRAIN	1994	9	−10.441	0.0134	15.9	<0.001	0.85
PFSRAIN	1995	9	−23.759	0.0260	20.4	0.002	0.77
PFSRAIN	1996	9	−2.194	0.0090	11.4	<0.001	0.92
FWTEMP	1991	8 [b]	4.243	−0.0039	35.9	0.032	0.56
FWTEMP	1992	8 [b]	4.972	−0.0047	26.5	0.009	0.70
FWTEMP	1993	8 [b]	4.756	−0.0042	30.7	0.018	0.64
FWTEMP	1994	8 [b]	3.088	−0.0040	36.6	0.034	0.55
FWTEMP	1995	8 [b]	7.354	−0.0048	21.9	0.004	0.78
FWTEMP	1996	8 [b]	5.866	−0.0041	32.4	0.021	0.62
ENTEMP	1991	8 [b]	12.990	−0.0055	28.0	0.012	0.68
ENTEMP	1992	8 [b]	14.982	−0.0063	26.7	0.010	0.70
ENTEMP	1993	8 [b]	12.759	−0.0052	31.9	0.020	0.62
ENTEMP	1994	8 [b]	14.440	−0.0061	26.7	0.010	0.70
ENTEMP	1995	8 [b]	11.598	−0.0056	26.4	0.010	0.70
ENTEMP	1996	7 [b, c]	15.062	−0.0061	25.6	0.011	0.75

[a] Defined in text above.

[b] Data unavailable from Sunspot Observatory, New Mexico.

[c] Data missing for April 1996 at one station.

[d] ns–non-significant at $\alpha = 0.05$.

APPENDIX 3.D
Energetic and Biomass Requirements of Mexican Spotted Owls

To describe the functional response of Mexican spotted owls to their common prey, I needed an estimate of the number of prey consumed during multiple breeding seasons. Dietary proportions alone only provided a relative measure based on collected pellets. Pellet collections from owl species that use multiple roosts typically do not represent total numbers of prey consumed because it is rare that all pellets are recovered (Petty 1999). Total numbers of prey consumed by different owl family units can therefore vary simply according to the different number of pellets collected among owl territories. The total number of each prey taken by owl family units during the breeding season could, however, be estimated from the dietary proportions given the total biomass consumed during that time (Lindén and Wikman 1983, Korpimäki and Norrdahl 1991). The latter can be estimated as a function of the amount of energy that would be required to sustain each owl family unit during the breeding season, in this case 184 days (Ward et al. 1998). The purpose of this appendix is to describe the model and associated assumptions used to estimate the owls' energetic requirements and in turn the amount of prey biomass consumed.

I modeled total energy required during the breeding season (E_B; kJ) as a sum of maintenance requirements (M_{EM}) likely incurred by an owl pair from which dietary samples were collected plus specific requirements for the level of reproduction (R_{EM}) exhibited by that pair in a given breeding season,

$$E_B = M_{EM} + R_{EM} \qquad (3.D.1).$$

Energetic costs for other needs or activities (e.g., molt, flight) were not included because inputs to related predictive equations (e.g., feather production and travel distances while foraging [Murphy1996, Norberg 1996] by these owls) were not available. Thus, energetic costs estimated herein are best considered minimum values most useful for comparing functional responses to different prey species.

M_{EM} was defined as amount of energy (kJ/d) required to sustain normal growth and repair beyond a basal metabolic rate and for thermostasis (Walsberg 1983, Carey 1996),

$$M_{EM} = B_{EM} + G_{EM} + Th_{EM} \qquad (3.D.2).$$

I used a basal metabolic rate (BMR) of 0.84 $ccO^2/g \cdot hr$ reported for Mexican spotted owls by Ganey et al. (1993), an average mass for male (509 g) and female (569 g) adult/subadult Mexican spotted owls reported by Gutiérrez et al. (1995), and relevant unit conversions (Carey 1996) to calculate metabolized energy (kJ/d) required during inactive (e.g., roosting, nesting) periods (B_{EM}). I calculated metabolized energy (kJ/d) required for normal growth and repair (G_{EM}) as $1.7 \cdot B_{EM}$ (King 1973). I estimated hourly thermoregulatory costs (kJ/hr; Th_{EM}) as a function of ambient temperature (C°; T_a) in the owl's normal roosting habitat given a linear, three-segmented model of oxygen consumption by Mexican spotted owls determined over a range of T_a manipulated above and below the thermal neutral zone (Ganey et al. 1993). Hourly T_a in the owl's roosting habitat were estimated using three steps. First, daily minimum and maximum temperatures were compiled from a cooperative weather station in Cloudcroft, New Mexico (Western Regional Climate Center, NOAA). These data were then converted to minimum and maximum temperatures expected in mesic forest habitat (the owl's normal roosting environment) using a predictive equation developed from simultaneous measurements during the study period (Fig. 3.D.1). Lastly, hourly T_a were estimated as hourly points along a cubic spline fitted through the daily maximum and minimum values observed at mesic forest sites. Hourly costs for thermogenesis were summed for each of the 184 days in the owl's six breeding seasons (1991-1996). Use of T_a rather than operative (T_e) or standard operative temperature (T_{es}) can underestimate thermoregulatory costs by ignoring the influence of radiation, convection, and humidity experienced by the organism (Bakken 1992). Underestimates using T_a are usually greatest for animals occurring in open environments during winter periods (Dawson and O'Conner 1996). I reduced the potential for committing such errors by using T_a taken from within the owl's roosting habitat which is a sheltered environment and applying this to the breeding season, a relatively warm period.

R_{EM}, was defined as the amount of metabolized energy (kJ) required to produce and raise the number of fledglings observed for a given pair of owls during a given year. This included costs for egg production (Eg_{EM}) and the youngs' growth over the usual period of provisioning by parents (~90 days; Gutiérrez et al. 1995),

$$R_{EM} = n \cdot (Eg_{EM} + Fl_{EM}) \qquad (3.D.3)$$

where n is the number of fledglings observed. Costs for spermatogenesis and incubation were considered negligible and therefore not included (Walsberg 1983).

The number of fledglings produced by a given owl pair during a given year was compiled from planned surveys conducted by USDA Forest Service personal from the Sacramento Ranger District (USDA 1990, Ward and Salas 2000). Cost for production of each egg was estimated as a product of egg mass (g), egg density (kJ/g), and efficiency of biosynthesis (Walsberg 1983),

$$Eg_{EM} = M_{egg} \cdot D_{egg} \,/\, Efficiency \qquad (3.D.4).$$

Because fresh mass of spotted owl eggs is unknown (Gutiérrez et al. 1995), I used the allometric equation of $0.277 \cdot M_b^{0.77}$ given by Walsberg (1983) to estimate an egg mass of 36.6 g produced by an average female weighing 569 g. Given an average whole egg density of 4.78 kJ/g for altricial species and a biosynthesis efficiency of 75% (Wijnandts 1984), I estimated the energetic cost of one egg to be 233 kJ. I assumed clutch sizes were equal to the number of fledglings observed during surveys because egg and hatchling survival rates for spotted owls were unknown. However, clutch sizes only vary from 1 to 3, with 4 eggs exceedingly rare (Gutiérrez et al. 1995). Hence, errors caused by unaccounted egg production would not amount to much. Total energetic cost (kJ) for fulfilling each fledgling's growth requirements was estimated from an equation given by Weathers (1991; his TEM model),

$$Fl_{EM} = 6.65 \cdot M_b^{0.852} \cdot t_{fl}^{0.710} \qquad (3.D.5),$$

where M_b, body mass of the fledgling following a 90-d growth period (t_{fl}), was set at 539 g (mid-point between mass of adult male and female Mexican spotted owls). Accordingly, amount of energy required per fledgling was estimated to be 34,486 kJ.

An estimate of E_B was converted to total biomass consumed (g) assuming that the owl's common prey (murid rodents) provided, on average, 18.4 kJ/g (Graber 1962) and that 75% of this energy was assimilated (Wijnandts 1984). Thus, E_B and total biomass consumed varied by breeding season according to changes in ambient temperature and number of young produced (Table 3.D.1). Specific numbers of each common prey genera consumed by each owl family unit during each breeding season were then estimated as a product of dietary proportions (% biomass) determined from pellet samples and total biomass consumed as determined above. The average number of each prey consumed during a breeding season was plotted against the average numbers available to produce corresponding functional responses shown in Figure 3.4.

Table 3.D.1. Energy required and total biomass consumed by Mexican spotted owls during six 184-day breeding seasons (March through August, 1991-1996) in the Sacramento Mountains, New Mexico. Values are means ± SE among owl families.

Year	Number of Owl Families	Number of Fledglings	Cost (kJ) of Reproduction	Total [a] Energy (kJ)	Biomass (g) Consumed
1991	16	1.69 ± 0.267	58,590 ± 9,385	215,322	15,603 ± 678
1992	8	1.38 ± 0.263	47,740 ± 9,133	200,777	14,559 ± 662
1993	14	0.50 ± 0.228	17,360 ± 7,932	173,292	12,557 ± 575
1994	3	0.66 ± 0.667	23,147 ± 23,147	178,282	12,919 ± 1,677
1995	6	0	0	156,206	11,319
1996	11	1.54 ± 0.207	53,658 ± 7,198	208,217	15,088 ± 522

[a] SE for total energy cost is the same as that for cost of reproduction.

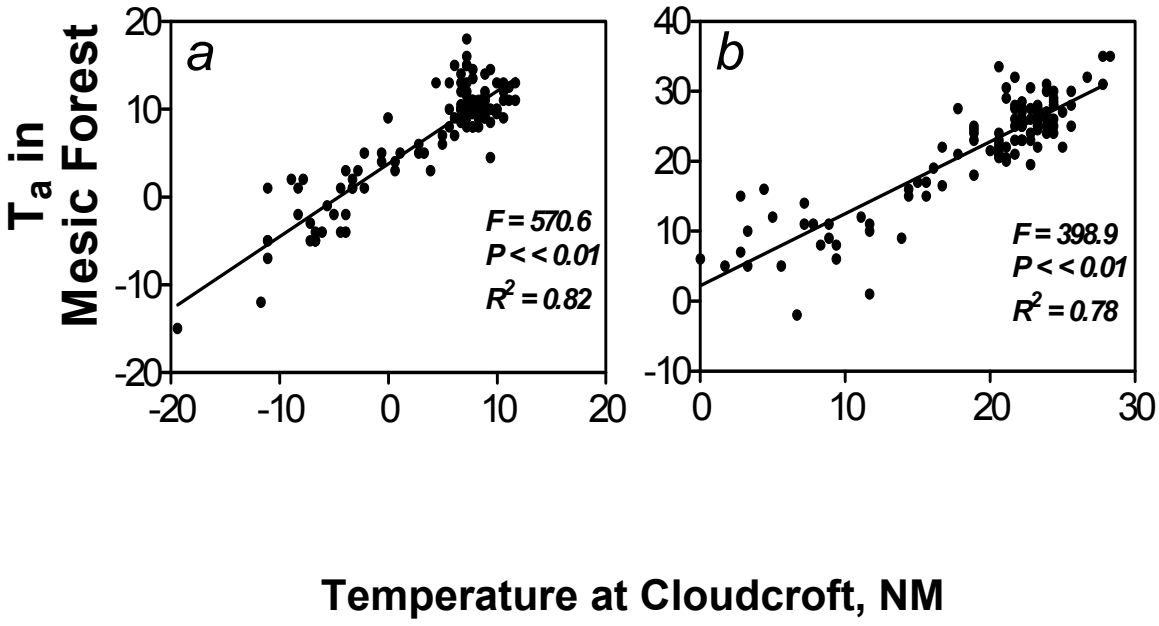

Figure 3.D.1. Linear relationships developed to predict minimum (*a*) and maximum (*b*) ambient temperatures (C°) in Mexican spotted owl roosting habitat from temperatures recorded at a weather station in Cloudcroft, New Mexico. Measurements of temperatures in mesic forests were taken at 6 different sites during 1991–1996.

APPENDIX 3.E
Items in Mexican Spotted Owl Pellets

Frequency of prey items found in pellets regurgitated by Mexican spotted owls during breeding periods (1991–1996) in the Sacramento Mountains, New Mexico.

Species	Owl Territory (1991)																					
	ZINK	FIRE	WIWH	PENW	SIXT	CHIP	BLUF	CRIS	RUSS	DRYB	JAMS	HIDD	GDSL	LHAY	SEVL	WILM	GRES	PEAK	NEWN	BENS	CARI	JIMJ
Sorex monticolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorex merriami	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0
Sorex spp.	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antrozous pallidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus cinereus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown bat	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvilagus spp.	0	0	0	0	4	1	1	0	0	1	0	0	0	0	0	1	1	2	1	1	1	0
Tamiasciurus hudsonicus	0	0	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tamias spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spermophilus tridecemlineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sciurid spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thomomys bottae	0	1	0	0	0	4	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Reithrodonotomys megalotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Peromyscus bolyii	2	13	1	1	14	3	2	1	0	1	1	1	0	3	1	11	8	3	8	4	2	0
Peromyscus maniculatus	3	7	0	0	16	9	11	4	1	3	2	0	0	2	8	9	19	4	11	10	4	0
Peromyscus nasutus	0	2	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0
Peromyscus spp.	1	1	3	1	4	7	1	1	0	1	6	2	2	1	2	6	14	0	5	4	0	0
Mus musculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma albigula	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma mexicana	1	9	2	0	10	0	1	3	0	1	1	0	0	1	1	3	6	0	2	1	1	0
Neotoma spp.	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Microtus mexicanus	1	0	2	0	2	1	4	1	1	0	0	0	0	1	1	1	1	0	0	1	0	0
Microtus longicaudus	1	1	0	0	2	1	3	3	0	0	2	0	0	0	1	1	0	4	1	2	0	0

APPENDIX 3.E (Continued).

Species	Owl Territory (1991)																					
	ZINK	FIRE	WIWH	PENW	SIXT	CHIP	BLUF	CRIS	RUSS	DRYB	JAMS	HIDD	GDSL	LHAY	SEVL	WILM	GRES	PEAK	NEWN	BENS	CARI	JIMJ
Microtus spp.	2	1	2	1	3	2	4	5	0	0	0	0	1	0	0	2	0	3	0	0	1	0
Small (<50 g) mammal	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Medium (50-100 g) mammal	1	3	0	0	5	0	3	5	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Larger (>100 g) mammal	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Unknown mammal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustela frenata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glaucidium gnoma	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small (<40 g) bird	0	3	0	0	3	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Medium (40-100 g) bird	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Larger (>100 g) bird	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown bird	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arthropod	0	11	0	0	10	4	1	3	0	2	1	1	0	2	0	1	7	2	0	1	1	0
Total	13	56	13	4	77	36	36	31	3	12	17	4	4	10	14	36	62	21	28	26	10	1

APPENDIX 3.E (Continued).

Species	Owl Territory (1992)												
	GOLF	RUSS	SEVL	WILM	JAMS	CHIP	HAYC	RANC	DRYB	LNEW	NEWM	LHAY	LWIL
Sorex monticolus	0	0	0	0	0	0	0	0	0	1	0	0	0
Sorex merriami	0	0	0	0	0	0	0	0	1	0	0	0	0
Sorex spp.	0	0	0	0	0	3	1	0	0	0	1	0	0
Antrozous pallidus	0	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus cinereus	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown bat	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvilagus spp.	0	0	1	3	0	1	2	1	4	1	0	1	0
Tamiasciurus hudsonicus	0	0	0	0	0	0	0	0	0	0	0	0	0
Tamias spp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Spermophilus tridecemlineatus	0	0	0	0	1	0	0	0	0	0	0	0	0
Sciurid spp.	0	0	0	0	0	0	0	2	0	1	0	0	0
Thomomys bottae	1	0	0	0	0	7	4	0	0	6	1	2	1
Reithrodonotomys megalotis	0	0	0	0	0	0	0	0	0	0	0	0	0
Peromyscus bolyii	0	0	0	1	0	0	2	0	0	5	0	2	1
Peromyscus maniculatus	0	0	0	14	0	2	2	9	0	4	0	5	1
Peromyscus nasutus	0	0	0	0	0	0	0	2	0	0	0	2	0
Peromyscus spp.	0	0	0	10	0	1	1	3	0	1	0	0	0
Mus musculus	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma albigula	0	1	0	1	0	1	1	0	0	0	0	1	0
Neotoma mexicana	0	0	0	2	3	2	1	1	0	2	0	0	0
Neotoma spp.	0	0	0	0	0	0	2	0	0	2	0	3	0
Microtus mexicanus	0	0	0	0	0	0	1	0	1	5	0	0	0
Microtus longicaudus	0	0	0	0	0	0	0	0	0	1	0	0	0
Microtus spp.	1	1	1	6	2	30	10	1	3	29	7	0	1
Small mammal (<50 g)	0	2	0	0	0	2	1	0	1	0	0	0	0
Medium mammal (50-100 g)	0	0	0	0	0	3	4	4	0	2	1	0	1
Larger mammal (>100 g)	0	0	0	0	0	0	1	0	0	0	1	1	1
Unknown mammal	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustela frenata	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 3.E (Continued).

Species	Owl Territory (1992)												
	GOLF	RUSS	SEVL	WILM	JAMS	CHIP	HAYC	RANC	DRYB	LNEW	NEWM	LHAY	LWIL
Glaucidium gnoma	0	0	0	0	0	0	0	0	0	0	0	0	0
Small bird (<40 g)	0	0	0	0	0	1	0	0	0	1	1	0	0
Medium bird (40-100 g)	0	1	0	0	1	1	3	1	0	1	1	0	0
Larger bird (>100 g)	0	0	0	0	1	1	0	0	0	0	0	0	0
Unknown bird	0	0	0	0	0	0	0	0	0	0	0	0	0
Arthropod	1	1	11	2	0	12	5	4	0	8	4	1	0
Total	3	6	13	39	8	67	41	28	10	70	17	18	6

APPENDIX 3.E (Continued).

Species	Owl Territory (1993)																
	BENS	CRKD	DRYB	RANC	FIRE	HAYC	ELPA	SIXT	WALK	LNEW	WWAL	CHIP	WILM	RAIL	GEOR	NEWM	POIS
Sorex monticolus	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0
Sorex merriami	0	0	0	0	0	0	2	0	0	5	0	3	7	0	0	0	0
Sorex spp.	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2	0
Antrozous pallidus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lasiurus cinereus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown bat	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvilagus spp.	1	5	4	4	0	0	2	1	0	1	14	1	0	0	1	0	0
Tamiasciurus hudsonicus	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0
Tamias spp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Spermophilus tridecemlineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sciurid spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Thomomys bottae	0	1	1	1	0	0	0	0	1	1	10	2	5	0	1	2	0
Reithrodonotomys megalotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peromyscus bolyii	0	8	5	8	0	0	1	2	1	3	9	0	1	0	0	6	0
Peromyscus maniculatus	3	5	11	4	0	0	1	14	9	1	16	1	1	0	1	11	2
Peromyscus nasutus	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	3
Peromyscus spp.	0	4	2	4	0	0	0	6	3	3	15	0	0	0	1	1	0
Mus musculus	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Neotoma albigula	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma mexicana	0	4	8	8	1	1	4	3	1	1	5	3	5	0	0	3	3
Neotoma spp.	0	8	4	0	1	0	1	0	0	0	5	0	2	0	0	0	0
Microtus mexicanus	2	0	2	4	0	0	1	5	3	16	5	3	5	2	1	22	4
Microtus longicaudus	3	1	2	1	1	0	5	4	2	16	16	6	24	2	0	20	0
Microtus spp.	4	1	6	3	0	0	5	4	11	5	13	6	15	0	2	18	5
Small mammal (<50 g)	4	1	3	0	0	0	0	6	2	3	1	0	7	3	0	2	0
Medium mammal (50-100 g)	0	3	3	4	1	0	1	1	1	3	7	1	10	0	6	1	0
Larger mammal (>100 g)	0	1	1	1	0	0	0	1	2	0	1	1	0	0	0	0	2
Unknown mammal	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Mustela frenata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glaucidium gnoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 3.E (Continued).

Species	Owl Territory (1993)																
	BENS	CRKD	DRYB	RANC	FIRE	HAYC	ELPA	SIXT	WALK	LNEW	WWAL	CHIP	WILM	RAIL	GEOR	NEWM	POIS
Small bird (<40 g)	0	2	0	2	1	0	0	0	0	1	3	0	0	0	0	1	1
Medium bird (40-100 g)	1	1	0	1	1	0	0	0	0	0	1	0	3	1	0	1	0
Larger bird (>100 g)	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Unknown bird	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arthropod	1	16	11	15	1	1	1	13	11	15	51	3	5	3	0	4	2
Total	19	64	65	64	7	2	25	65	49	75	173	32	94	11	13	95	22

APPENDIX 3.E (Continued).

Species	Owl Territory (1994)									
	AFRA	PETS	GOCO	ELPA	SIXT	NEWM	BENS	HAYC	LNEW	RANC
Sorex monticolus	0	1	0	0	0	0	0	0	4	0
Sorex merriami	0	0	0	0	0	0	0	0	0	0
Sorex spp.	0	0	0	0	0	0	0	0	0	0
Antrozous pallidus	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	0	0	0	0	0	0	0	0	0	2
Lasionycteris noctivagans	0	0	0	0	0	0	0	0	0	0
Lasiurus cinereus	0	0	0	0	0	0	0	0	0	0
Unknown bat	0	0	0	0	0	0	0	0	0	0
Sylvilagus spp.	1	0	1	0	0	2	1	1	0	0
Tamiasciurus hudsonicus	0	0	0	1	0	2	0	0	1	0
Tamias spp.	0	0	0	0	0	0	0	0	0	0
Spermophilus tridecemlineatus	0	0	0	0	0	0	0	0	0	0
Sciurid spp.	0	0	0	0	0	0	0	0	0	0
Thomomys bottae	0	0	0	0	0	1	0	0	1	1
Reithrodonotomys megalotis	0	0	0	0	0	0	0	0	0	0
Peromyscus bolyii	0	0	0	0	0	0	0	0	0	3
Peromyscus maniculatus	0	0	0	6	1	11	11	2	14	0
Peromyscus nasutus	0	0	0	0	0	0	0	0	0	0
Peromyscus spp.	0	1	2	0	0	1	0	0	0	2
Mus musculus	0	0	0	0	0	0	0	0	0	0
Neotoma albigula	0	0	0	0	0	0	0	0	0	0
Neotoma mexicana	2	2	0	1	2	2	1	0	1	1
Neotoma spp.	0	0	1	0	1	1	0	0	1	0
Microtus mexicanus	0	0	0	0	0	1	0	0	0	0
Microtus longicaudus	0	1	1	1	4	5	3	1	13	0
Microtus spp.	0	0	0	0	0	0	0	0	0	1
Small mammal (<50 g)	0	0	0	0	0	0	0	0	0	0
Medium mammal (50-100 g)	0	0	0	0	0	0	0	0	0	0
Larger mammal (>100 g)	0	0	0	0	0	1	0	0	0	0
Unknown mammal	0	0	0	0	0	0	0	0	0	0
Mustela frenata	0	0	0	0	0	0	0	0	0	0
Glaucidium gnoma	0	0	0	0	0	0	0	0	0	0

APPENDIX 3.E (Continued).

Species	Owl Territory (1994)									
	AFRA	PETS	GOCO	ELPA	SIXT	NEWM	BENS	HAYC	LNEW	RANC
Small bird (<40 g)	0	0	0	0	0	0	0	0	1	2
Medium bird (40-100 g)	0	0	0	0	0	0	0	0	1	0
Larger bird (>100 g)	0	0	0	0	0	0	0	0	0	0
Unknown bird	0	0	0	0	0	0	0	0	0	0
Arthropod	0	0	0	0	0	0	0	0	0	0
Total	3	5	5	9	8	27	16	4	37	12

APPENDIX 3.E (Continued).

Species	Owl Territory (1995)														
	HIDD	SULL	GDSL	TRAL	SEVL	PEPP	WWAL	POTA	NEWM	DRYB	SIXT	BEAR	GRES	SNAP	DELW
Sorex monticolus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sorex merriami	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorex spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antrozous pallidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus cinereus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown bat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvilagus spp.	0	0	0	0	0	0	0	0	0	3	2	3	0	0	1
Tamiasciurus hudsonicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tamias spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Spermophilus tridecemlineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sciurid spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thomomys bottae	0	0	1	0	1	3	0	1	0	2	0	1	0	0	0
Reithrodonotomys megalotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peromyscus bolyii	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Peromyscus maniculatus	1	1	6	1	2	2	1	2	0	4	9	1	3	1	0
Peromyscus nasutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peromyscus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mus musculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma albigula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma mexicana	0	0	2	0	2	2	0	0	1	1	3	1	0	0	0
Neotoma spp.	1	0	1	0	2	0	1	0	0	2	0	1	2	2	0
Microtus mexicanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microtus longicaudus	1	0	5	0	1	4	0	1	1	2	0	3	0	0	0
Microtus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small mammal (<50 g)	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0
Medium mammal (50-100 g)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larger mammal (>100 g)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown mammal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustela frenata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glaucidium gnoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 3.E (Continued).

Species	Owl Territory (1995)														
	HIDD	SULL	GDSL	TRAL	SEVL	PEPP	WWAL	POTA	NEWM	DRYB	SIXT	BEAR	GRES	SNAP	DELW
Small bird (<40 g)	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0
Medium bird (40-100 g)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larger bird (>100 g)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown bird	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arthropod	0	1	1	0	1	0	1	0	1	1	0	2	0	0	0
Total	3	2	17	2	11	15	3	4	4	15	16	12	5	3	2

APPENDIX 3.E (Continued).

Species	Owl Territory (1996)																	
	BEAR	BLUF	CARI	DRYB	GDSL	HIDD	HYAT	LHAY	MAST	MOOR	POTA	RUSS	SPRG	SULL	TELE	TRAL	WAYL	WILM
Sorex monticolus	0	1	0	0	1	0	0	0	0	4	1	0	0	0	3	0	0	0
Sorex merriami	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorex spp.	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Antrozous pallidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus fuscus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasionycteris noctivagans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasiurus cinereus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown bat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvilagus spp.	1	6	1	2	0	2	0	0	1	0	1	1	1	1	1	0	0	2
Tamiasciurus hudsonicus	0	1	0	1	0	0	0	1	1	2	0	0	2	0	0	1	0	0
Tamias spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spermophilus tridecemlineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sciurid spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thomomys bottae	2	0	0	5	0	1	0	0	3	3	0	4	6	1	1	0	0	2
Reithrodonotomys megalotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peromyscus bolyii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peromyscus maniculatus	2	1	0	2	0	1	2	0	3	2	5	0	0	0	1	0	0	3
Peromyscus nasutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peromyscus spp.	7	1	0	5	0	9	4	0	9	6	15	1	10	1	6	2	1	7
Mus musculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma albigula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotoma mexicana	3	2	1	3	0	1	1	0	4	1	1	0	3	0	0	1	0	2
Neotoma spp.	2	1	0	4	1	1	1	1	3	3	0	1	4	0	2	2	0	6
Microtus mexicanus	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Microtus longicaudus	2	3	0	1	2	4	0	0	5	4	2	1	2	0	2	0	0	4
Microtus spp.	7	3	0	3	3	0	1	0	3	3	2	0	2	1	1	0	2	2
Small mammal (<50 g)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Medium mammal (50-100 g)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Large mammal (>100 g)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Unknown mammal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mustela frenata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glaucidium gnoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 3.E (Continued).

Species	Owl Territory (1996)																	
	BEAR	BLUF	CARI	DRYB	GDSL	HIDD	HYAT	LHAY	MAST	MOOR	POTA	RUSS	SPRG	SULL	TELE	TRAL	WAYL	WILM
Small bird (<40 g)	1	1	0	0	0	0	0	0	0	4	0	0	2	0	0	0	0	0
Medium bird (40-100 g)	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Large bird (>100 g)	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Unknown bird	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arthropod	2	0	0	2	1	2	1	0	0	3	0	1	2	0	1	1	0	0
Total	30	21	3	29	8	21	11	2	35	36	29	9	35	4	18	9	3	28

APPENDIX 3.F
Sources of Small Mammal Mass

Small mammal mass (g) estimated from individuals captured during July through August (1991–1996) in the Sacramento Mountains, New Mexico. Sexes and age classes combined.

	1991			1992			1993			1994			1995			1996		
Species	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*
Sorex monitcolus	5.1	0.12	39	6.7	0.17	103	7.5	0.41	18	5.9	0.20	65	5.8	0.18	90	6.5	0.35	24
Tamias canipes	58.4	1.34	76	68.7	0.83	99	69.0	2.57	53	65.6	1.15	52	68.7	1.21	38	64.9	1.02	28
Peromyscus boylii	23.6	0.62	99	25.2	0.41	274	22.9	0.48	141	20.9	0.59	127	23.4	0.73	62	21.4	0.80	16
Peromyscus maniculatus	15.8	0.17	764	18.6	0.22	449	18.5	0.26	293	16.5	0.18	590	17.1	0.35	179	17.8	0.30	206
Neotoma mexicana	112.8	7.38	28	118.9	5.16	78	113.2	5.82	55	116.4	7.02	38	119.2	5.90	41	107.6	8.65	29
Microtus mexicanus	26.7	1.14	48	30.2	0.27	981	27.2	0.43	371	26.9	0.63	266	26.0	0.42	337	28.3	0.98	117
Microtus longicaudus	30.8	1.22	90	34.3	0.54	501	32.4	0.61	226	32.4	1.31	81	31.8	2.37	24	33.1	1.24	91

APPENDIX 3.F (Continued)**.**

Sources of mass (g) of prey species not commonly captured during 1991 through 1996 in the Sacramento Mountains, New Mexico.

Species	x̄	± SE	*n*	Source
Sorex merriami	7.8	0.29	30	Captures, this study (all time periods combined).
Antrozous pallidus	17.8	0.74	30	Museum of Southwestern Biology, Univ. New Mexico.
Eptesicus fuscus	17.6	0.44	30	Museum of Southwestern Biology, Univ. New Mexico.
Lasionycteris noctivagans	10.5	0.36	30	Museum of Southwestern Biology, Univ. New Mexico.
Lasiurus cinereus	24.6	1.11	30	Museum of Southwestern Biology, Univ. New Mexico.
Sylvilagus sp.	125.0	----	--	Mid-point between plausible range of 50-300 g.
Tamiasciurus hudsonicus	171.5	10.31	12	Captures, this study (all time periods combined).
Spermophilus tridecemlineatus	101.0	13.08	10	Vertebrate Museum, New Mexico State University.
Thomomys bottae	96.4	3.49	47	Vertebrate Museum, New Mexico State University.
Rethrodontomys megalotis	11.8	1.45	11	Vertebrate Museum, New Mexico State University.
Peromyscus nasutus	28.5	3.74	62	Vertebrate Museum, New Mexico State University.
Mus musculus	22.0	----	1	Captures, this study (all time periods combined).
Neotoma albigula	161.1	5.80	30	Vertebrate Museum, New Mexico State University.
Mustela frenata	203.8	----	2	Vertebrate Museum, New Mexico State University.
Glaucidium gnoma	65.0	----	--	Johnsgard (1988).
Small bird	28.0	----	--	Steenhof (1983).
Medium bird	70.0	----	--	Approximation.
Large bird	120.0	----	--	Approximation.
Arthropod	1.0	----	--	Approximation.

CHAPTER 4

CURRENT PREY RELATIONSHIPS AND HISTORICAL HABITAT CONDITIONS: IMPLICATIONS FOR CONSERVING MEXICAN SPOTTED OWLS

The purpose of this investigation was to evaluate the hypothesis that Mexican spotted owls (*Strix occidentalis lucida*) can be conserved by manipulating microhabitat conditions that increase the abundance of one or more common prey species. I evaluated this hypothesis by (1) determining which common prey were preferred by this owl, (2) which prey species were most likely to influence the owl's reproduction, and by (3) assessing which prey species were most likely to increase in abundance following microhabitat manipulation. The investigation focused on one population of Mexican spotted owls over a 6-year period (1991–1996) in the Sacramento Mountains, New Mexico; an area where vegetation communities have been modified extensively over the past 100 years (Kaufmann et al. 1998, Chapter 1)

According to dietary analyses, I found that five murid rodents were most common among the variety of prey species consumed during the breeding season. These included the deer mouse (*Peromyscus maniculatus*), brush mouse (*P. boylii*), Mexican vole (*Microtus mexicanus*), long-tailed vole (*M. longicaudus*), and the Mexican woodrat (*Neotoma mexicana*). Depending on the year of study, the five species accounted for 53–77 % of frequency of all items recovered from samples of regurgitated pellets and

41–66 % of biomass consumed in the same samples (see Chapter 3, Tables 3.3 and 3.4).

Comparing dietary proportions of the owl's common prey to proportions estimated to occur in the owl's foraging areas, I found that mice and voles were captured in equal proportion to their availability and that woodrats were selected (i.e., taken in greater proportions relative to availability). When prey selectivity indices were examined relative to the extent of food surplus, woodrats appeared to be preferred over mice and voles. In addition, absolute functional responses revealed that (1) maximum numbers of woodrats were taken by Mexican spotted owls when their available numbers were at moderate levels (i.e., a concave-shaped response), (2) mice were taken at a consistent rate with increases of available numbers (i.e., a linear response), and (3) the number of voles taken decreased proportionally with increases of absolute numbers in the owl's foraging area (i.e., a positive but depreciating curvilinear response; see Chapter 3, Fig. 3.4). According to the owl's feeding preference, the Mexican woodrat appeared to be the most logical target prey species to manipulate (see Chapter 3).

The analysis of environmental factors (i.e., weather, habitat condition, and available prey biomass) that influenced the owl's reproduction, however, suggested a different target for conservation. Reproduction of Mexican spotted owls in the Sacramento Mountains appeared to be influenced most by total available biomass of four smaller species of prey. These included deer mice, brush mice, Mexican voles and long-tailed voles. Available biomass of Mexican woodrats was not correlated with the owl's reproductive potential nor its annual reproductive output (see Chapter 3, Table 3.8).

Thus, the dietary and reproductive responses by these spotted owls suggests two different management strategies. For one strategy, increasing the availability of a single

prey species, the Mexican woodrat, is identified as a potential management target, while another tact would be to maintain the availability and diversity of small prey. As stated in Chapter 1, dependence on a single prey species would render the greatest support for the original hypothesis of whether Mexican spotted owls could be conserved by manipulating habitat for its prey. From the land managers perspective, success in increasing the abundance of a single prey species through microhabitat manipulation is more feasible than increasing the abundance of several species or manipulating prey diversity. The reason is, that the diversity of these small mammals is not only associated with microhabitat structure within a macrohabitat type but also on the distribution of macrohabitat types (Chapter 2, Fig. 4.1), which cannot be altered readily.

The study hypothesis was also evaluated according to the factors that influence availability of the five common prey species (Chapter 2). A focus on abundance factors indicated that biomass (g/ha) of the two mouse species would be difficult to influence through microhabitat manipulation. For example, abundance of brush mice was strongly associated with rocks and shrub-like oaks (see Chapter 2, Table 2.23). It would be inefficient to supply rocks over large areas. More logically, abundance of low-growing species, like gray (*Quercus grisea*) or wavy-leaf oaks (*Q. undulata*) might be stimulated by hot-burning fire (Wood and Scanlon 1993, Baron 1999, Fule et al. 2000). However, hot-burning fires will usually not be practical to prescribe. Similarly, only two microhabitat variables were identified as factors associated with abundance of deer mice. One of these, the number of mature conifers (an indicator of greater seed production), could be enhanced through thinning young, excessively stocked stands. Although possible, stimulating greater production of conifer seed by reducing competition among

particular conifers could take considerable time to realize and outcomes would likely be less predictable, given the variability of annual weather patterns in this region. The second microhabitat factor was production of grasses and forbs. This attribute could be managed in part by regulating grazing in relevant habitats. Unfortunately, this factor was not found to be as strongly associated or as consistent an influence as cold temperatures during the fall and winter months or the number of mature female deer mice in a population. Obviously, the former is beyond control and the latter not likely to be manipulated directly by resource managers.

In contrast, abundance of both vole species appeared more likely to be influenced by microhabitat manipulation because of strong positive associations with grass and forb cover, particularly height of herbaceous plants. This attribute can be manipulated in part by regulating grazing of domestic ungulates (Birney et al. 1976, USDI 1991; 1995).

The potential to manipulate abundance of Mexican woodrats falls somewhere in between that of mice and voles. Although two vegetative microhabitat variables, density of shrubs and volume of large (>30-cm diameter) logs, were identified, these habitat associations with this woodrat's abundance were only moderately strong and their mathematical forms were not well defined (see Chapter 2, Table 2.23 and Fig. 2.20). According to natural-history studies, Mexican woodrats consume foliage from a variety of shrubs and often use large logs for protective cover while traveling or, when conditions permit, for dens (see review in Chapter 2:62–63). Shrubs can likely be stimulated through thinning or prescribed fire (Severson and Rinne 1988) but large downed logs that have characteristics matching those likely suitable to Mexican woodrats (e.g., with decay, rot, and cavities) may take hundreds of years to restore (Maser and Trappe 1984). In

overstocked stands at sites with high growth potential, thinning may allow such structures to develop over long periods of time. However, short-term surrogates may be added in the form of slash-piles created during thinning operations (Goodwin and Hungerford 1979) or by felling and leaving on site decaying or diseased trees. These features seem more feasible to manipulate than those found to be associated with abundance of either mouse species but less feasible compared to manipulating grass-forb cover, which affects abundance of both vole species.

Consequently, the study hypothesis may be strongly or weakly supported depending upon which of the owl's common prey is considered. This underscores the need for a clearer understanding of how particular prey may influence the owl's population processes.

In Chapter 3, I suggested that despite the lack of correlation with the owl's reproduction, availability of Mexican woodrats may be critical for the owl's survival. In an attempt to explain why spotted owls in the Sacramento Mountains may have adopted a preference for this prey, I speculated that biomass of Mexican woodrats may have provided a consistent staple for meeting energetic maintenance through periods when the smaller, common prey were not plentiful enough to support reproduction. This strategy possibly allowed these Mexican spotted owls to for go reproduction during lean times and to survive to subsequent breeding seasons when conditions would be more favorable. This type of 'bet-hedging' strategy appears common in moderate to long-lived raptors (Stearns 1976, Boyce 1988) and has been suggested elsewhere to describe life-history traits of northern spotted owls (*S. o. caurina*; Franklin et al. 2000).

I also suggested that the current preference for woodrats by spotted owls in the

study area could be a relic behavior from conditions when Mexican woodrats were more available and therefore increased not only the owl's likelihood of survival but also reproduction. The purpose of this chapter is to explore further the possibility that extensive alteration of the owl's foraging habitat in the Sacramento Mountains may have shifted the dynamics of the owl's common prey in a way that has affected the owl's reproduction. Following this assessment, I offer recommendations for designing experimental management that (1) is predicted to enhance future conditions for Mexican spotted owls in the Sacramento Mountains and (2) provides additional information for evaluating this prediction.

Historical Landscape Condition

In the Sacramento Mountains, Mexican spotted owls concentrate their foraging, roosting, and nesting in mixed-conifer forest (Zwank et al. 1994, Ganey and Dick 1995, Ward et al. 1995, Ganey et al. *in review*, see also Chapter 3, Appendix 3.B). The mesic forest habitat sampled as part of the present investigation was comprised of this forest type. Dominant tree species were Douglas-fir (*Psuedotsuga menziesii*) and white fir (*Abies concolor*). Other common conifers included southwestern white pine (*Pinus strobifomis*) and ponderosa pine (*P. ponderosa*) (see Chapter 1, Appendix 1.A for additional plant associations). The vast majority (>90%) of this forest type exists in a mid-seral stage (60–100 yrs), primarily as a consequence of extensive and intensive commercial timber harvest occurring during 1903–1941 (Kaufmann et al. 1998). For example, 3,480 ha of mixed-conifer and ponderosa pine forest were clear-cut harvested by 1906 (Holmes 1906; Fig. 4.2). Diameters of harvested trees >50 cm were common. The area harvested was a function of railroad access and therefore systematic and

chronological on the landscape (Glover 1984). Trees were harvested first in the vicinity of Cloudcroft, New Mexico, and continued southward with time as rail lines spanned farther into the mountain valleys (Kaufmann et al. 1998:Fig. 12). Harvest methods were thorough, leaving some residual seed trees (≤30 cm), but after the Alamogordo Lumber Company decided to sell the cut lands to the Federal Government and regeneration was considered less important, the tree size limit was reduced further (Kaufmann et al. 1998). During the past century, fires also modified portions of this landscape, as did grazing by substantially greater numbers of livestock than witnessed today, and agriculture in many of the mountain valleys and stream corridors (Kaufmann et al. 1998, Chapter 1). In addition, the policy of suppressing all fires was initiated in the 1940's and popularized in the 1950's. Fire suppression has likely contributed greatly to the current structure of vegetative communities in the Sacramento Mountains by reducing mortality of young trees and swaying competition with shrubs and herbaceous plants (Zimmerman and Neuenschwander 1984, Kaufmann et al. 1998, Brown et al. 2001,).

For Mexican spotted owls, extensive clear-cut timber harvesting combined with fire suppression likely posed the most significant source of habitat alteration. Currently, less than 5% of the mixed-conifer forests in the Sacramento Mountains are in a late-seral state, whereas 10% to 26% are believed to have been in an “old-growth” (late seral) state in 1880 (Regan 1997). The majority of all conifer forest stands were comprised of larger, more widely spaced trees than are present today (Kaufmann et al. 1998). Consequently, the structure of what I have labeled as a mesic forest habitat has changed from a stand with greater density of large trees with wider spacing, multiple vertical layers, heterogenous mosaic of canopy gaps, greater decadence, and more large downed logs to

an excessive abundance of densely-stocked trees of smaller diameter (Fig. 4.3, see also Kaufmann et al. 1998:Fig. 26). Current mid-seral stages of mesic forest have closed (>70%) canopy but are less complex structurally compared to late-seral conditions and likely include slightly more Douglas-fir than existed historically (Kaufmann et al. 1998:Fig. 24).

Predictions

Several scenarios can be hypothesized to describe the potential effects of past habitat change on Mexican spotted owls occurring in the Sacramento Mountains. Initially, extensive removal of large trees likely reduced nesting and roosting structures, creating unfavorable microclimates. Extensive opening of canopy likely reduced suitable foraging habitat and may have increased risk of predation by other raptors (Gutiérrez et al. 1996, Ganey et al. 1997). However, following vegetative succession to the present condition, it is clear that Mexican spotted owls have found residual microsites that are suitable for roosting and nesting (Zwank et al. 1994, Ganey and Dick 1995, Ganey et al. 2000). Foraging habitat appears sufficient to permit survival and reproduction. In addition, recent estimates of density of Mexican spotted owls in the Sacramento Mountains are comparable to other high-density populations of the species (Ward et al. 1995). One interpretation of these patterns is that numerically the Sacramento Mountain population of Mexican spotted owls was not impacted heavily over the long-term by extensive habitat alteration.

However, what may have changed, is the magnitude of temporal variation in demographic rates rather than their mean values. In particular, reproductive output may have become more erratic as a function of habitat-induced shifts in prey composition and

dynamics. For example, early and mid-seral stages may now support great abundances or periodic irruptions of rapid-colonizing species like Mexican voles (Davis and Callahan 1992) or habitat generalists like the deer mouse (Sullivan and Krebs 1981, Van Horne 1981, Kirkland 1990). Greater consumption of small prey species that fluctuate widely over short periods of time (2-4 yrs) could contribute to greater temporal variation in the owls' reproductive rates and, ultimately, population numbers (Korpimäki 1986).

For this explanation to apply to Mexican spotted owls dwelling in the Sacramento Mountains, then: (1) microhabitat structures associated with Mexican woodrat availability should have diminished as a result of timber harvest and succession to a mid-seral stage, (2) Mexican woodrat availability should have diminished also while alternative (less preferred) prey increased in availability, and (3) less use of woodrats should be associated with greater temporal variation in the owl's reproductive output.

METHODS

I examined data from two sources to evaluate whether forest alteration may have contributed to wide temporal variation of spotted owl reproduction in the Sacramento Mountains. From the present study, I examined microhabitat features and small-mammal abundance data gathered from one mesic forest mid-seral site (DELW; elevation range of sample points: 2552–2591 m) and one late-seral site (GDSL; 2704–2759 m). The late-seral forest site was approximately 160 m higher in elevation. I limited the analysis to data from these two sites because both were sampled simultaneously over three consecutive summers (1994–1996) to estimate common prey abundance. Details describing the study area, site selection, and methods used to sample microhabitat features and small mammal abundance are described in Chapter 2. From published

literature and one public technical report, I gathered estimates of reproductive output and prey biomass consumed by spotted owls occurring at eight locations (Appendix 4.A). I chose studies that examined diet and reproductive output in the same population during identical or overlapping time periods. The number of years reporting reproductive data ranged from 4 to 8 years. The earliest period of consideration extended from 1987–1992 and the latest period extended from 1991–1996. Estimates of prey biomass (%) consumed were limited to breeding-season diets. Numbers of prey items from each study ranged from 278 to 8,169 collected from 11 to 151 spotted owl territories.

Analysis of these data allowed me to assess the three expectations described above. However, because site replication was lacking, any inferences should not be considered unequivocal. Rather, I draw on the results primarily to propose a working hypothesis to be tested experimentally, ideally through future manipulations of forest structure.

Data Analysis

I conducted a series of statistical comparisons between mid-seral and late-seral mesic forest to evaluate each expectation. I focused on two microhabitat features, shrub evenness and volume of large (>30-cm diameter) logs, to assess the potential impacts of forest alteration on features used by Mexican woodrats. Both of these variables showed modest positive correlations with Mexican woodrat biomass (see Chapter 2, Fig. 2.20). Shrub evenness provided an index of the woodrat's food abundance and volume of large downed logs quantified amounts of cover. I would expect suitable habitat for Mexican woodrats to increase with amounts of both features. Thus, under the given hypothesis, the mid-seral stage should have significantly less evenness of shrubs and less volume of

large logs. I used a Student's t-test with Type I error set at $\alpha = 0.05$ to provide a probability that the mid-seral site had fewer key habitat features for Mexican woodrats. Variation of values at each 4-ha sampling area (i.e., within a trapping grid, n =121 stations per grid) was used to estimate sampling variances. When the latter were found to be unequal according to an F-test, I calculated an approximated t-statistic and evaluated significance with Satterthwaite's (1946) calculation of degrees of freedom (SAS 2000).

Using data on the owl's three most common prey species that occur in mid-seral and late-seral mesic forest (deer mice, long-tailed vole and Mexican woodrat), I conducted two analyses to assess if forest modification may have diminished woodrat abundance and increased abundance of smaller prey like deer mice or long-tailed voles. In one analysis, I quantified biomass per unit of area (g/ha) for each species in each of three summers (1994–1996) at the same mid-seral site and late-seral site used to compare shrub evenness and volume of large logs. To evaluate probability of difference between the two seral stages, I conducted a z-test (White et al. 1982:139) on summer biomass per unit area from both sites during each year. In this case I designated a Type I error of $\alpha = 0.10$ to provide slightly greater power in rejecting a test of no difference and to be consistent with procedures used in Chapter 2. In the second analysis of these data, I calculated available biomass (kg) at different areas of macrohabitat presumed to be available to foraging owls. The areas ranged from 10 ha to 320 ha and increased by 10-ha increments. Under the hypothesis, significant reduction of late-seral area should have diminished Mexican woodrat abundance. Graphs of these results would identify the amount of area of each seral stage at which tradeoffs in biomass of the different prey groups would occur. For the calculations, I used an average biomass among the three

summers (1994–1996). Multiplying the 3-year average with each habitat area amount provided an estimate of available prey biomass. A total amount of 320 ha of mesic forest was assumed for these calculations according to average amounts observed for radio-marked male spotted owls during the breeding season (Chapter 3:Appendix 3B). Mid-seral forest amounts were set to equal the difference between 320 ha and the amount of late-seral mesic forest assigned in each calculation. For example, when calculating amount of woodrat biomass (kg) available in a foraging range comprised of 10 ha of late seral forest, the mid-seral area would be set at 310 ha and these two area amounts would be multiplied by the respective estimates of woodrat biomass per unit area.

Using information from previous studies, I plotted and quantified temporal variation in reproductive output by spotted owls as a function of woodrat biomass (%) or the combined biomass of mice and voles consumed by owls in the same population. If female fecundity was reported rather than the mean number of young per pair adequately checked, I multiplied the fecundity value by 2 to get mean reproductive output ($\bar{RO}_i$) for a given year *i*. Here, I assumed a 50:50 sex ratio for young, which has been found to be reasonable in those populations that have been studied (Franklin et al. 1996).

I used a coefficient of variation of the mean annual reproductive output averaged over the years given for each study to quantify temporal variation ($CV_t\ [\bar{\bar{RO}}]$ in %). This measure of variance accounted for any increases in variation attributed to the size of the mean and was estimated as

$$CV_t\ [\bar{\bar{RO}}] = \frac{\sqrt{\hat{var}_t[\bar{\bar{RO}}]}}{\bar{\bar{RO}}} \cdot 100\%$$

where temporal variance of the mean reproductive output for all years examined ($\hat{var}_t[\bar{\bar{RO}}]$) was estimated by (1) averaging the sampling variances associated with mean reproductive output of each year, then (2) subtracting this average sampling variance from the total variance associated with $\bar{\bar{RO}}$ (Burnham et al. 1987). Prior to estimating regression statistics, I transformed $CV_t\ [\bar{\bar{RO}}]$ and biomass proportions using an arcsine-square root function (Zar 1984:239) to meet the assumption of normality. Under the hypothesis, reproductive output by spotted owls should be more consistent for those owls consuming greater amounts of woodrat biomass. Thus, the slope of this relationship should be negative and greater than zero. An opposite trend should be noted for the relationship with mice and voles.

RESULTS AND DISCUSSION

In evaluating each of the three expectations under the hypothesis that past forest alteration has affected the dynamics of Mexican spotted owl reproduction, I found that none of the tests refuted the hypothesis. First, both microhabitat variables previously known to be correlated with biomass of Mexican woodrats, shrub evenness and large log volume, were significantly greater at the late-seral mesic forest site (shrub evenness: t = -4.66, df = 176, $P < 0.001$; large log volume: t = -4.02, df = 201, $P < 0.001$; Fig. 4.4).

Second, summer biomass of deer mice was significantly greater at the late-seral site during all three summers (Fig. 4.5a). Summer biomass of long-tailed voles was similar at the two sites during 1994 and 1995, but significantly greater at the late-seral site during 1996 (Fig. 4.5b). Summer biomass of Mexican woodrats showed a similar pattern to that of the long-tailed vole, being significantly greater at the late seral forest site during 1996 (Fig. 4.5c). However, summer biomass of long-tailed voles changed by a

factor of 10 between 1995 and 1996, whereas that of Mexican woodrats changed only by a factor of 3. The amount of Mexican woodrat biomass was projected to be equal in both seral stages (14.2 kg) when, on average, the owl's 320-ha foraging range included 105 ha of late-seral mesic forest (Fig. 3.6a). In contrast, the combined amount of mouse and vole biomass was projected to be equal in both seral stages (52.0 kg) at 165 ha of late seral forest (Fig. 3.6b), and biomass of all five common prey species was approximately equal (67 kg) at 150 ha of late seral forest (Fig. 3.6c). For the maximum conversion of 320 ha of late seral forest to mid-seral condition, 22.3 kg of woodrat biomass would be lost while 9.2 kg of small prey biomass (primarily deer mouse) would be gained (see horizontal lines in Figs. 4.4a and b). When biomass of the five common prey are considered, the net loss would be 13.1 kg (Fig. 4.4c). From these data, the greatest influence of forest alteration appears to be a reduction in Mexican woodrat biomass.

On average, biomass consumed and temporal variation in the owl's reproduction $CV_t\ [\bar{\bar{RO}}]$ across different regions was negatively associated with the amount of woodrat biomass consumed by these owls (Fig. 4.7*a*). The linear slope (β_1) was negative and statistically different from zero (95% CI [β_1] = −0.941 to −0.163). In contrast, the consumption of smaller prey tended to be positively associated with greater variability in the owl's reproductive output (Fig. 4.7b). However, the slope of the association was not statistically different from zero.

Collectively, these findings support the working hypothesis. In the Sacramento Mountains, progression from a landscape with formerly greater amounts of late-seral conifer forest to one predominated by a structurally different mid-seral state has reduced the availability of the owl's preferred prey, Mexican woodrats. Greater reliance on small

prey like mice and voles that undergo more rapid and dynamic population change appears to have contributed to increased variance in reproductive output by these owls over time.

Certainly, other factors can cause temporal variability in the owl's reproductive output. Weather, including precipitation during the nesting season (Zabel et al. 1996, Franklin et al 2000, North et al. 2000) or during a previous fall through spring (Wagner et al. 1996), and cold temperatures during April (North et al. 2000) have been inversely correlated with the production of spotted owl young. These relationships have been attributed to a reduction in prey access and/or an increase in energetic cost to spotted owls. When modeling weather effects on Mexican spotted owl reproduction, I found only weak evidence for an influence by precipitation during the nesting period and minimum temperatures during fall–winter (see Chapter 3, Table 3.7). I found much stronger evidence for temporal covariation between the owl's reproductive output and availability of its common prey (see Chapter 3, Table 3.8). It is likely that weather, habitat condition, the owl's population structure, and prey availability all interact to influence variation in the owl's reproductive performance. The interaction among these factors is complex (see discussions by Franklin et al. 2000, North et al.2000). In the present study, available prey biomass appeared to have the most detectable influence.

Other studies of *Strix* owls have also implicated the effect of habitat alteration on owl populations through effects on prey distribution and abundance. Petty (1999) found that tawny owls (*Strix aluco*) occupying planted spruce (*Picea sitchensis* and *P. abies*) forests near Kielder in northern England responded functionally to shifts in prey availability on a landscape scale. These forests were managed with a rotational clear-cutting system (40–60 yr) that created a mosaic of different aged stands and patches

ranging from 5 ha to >100 ha in size. Field voles (*Microtus agrestis*; ~40 g) that dwelled in cut-over areas (10-15 yr in age) and underwent multi-annual fluctuations in abundance were a primary prey species during the 19-year study. Overall, field voles comprised 80% of the biomass identified in tawny owl pellets and 47% identified in remains at their nests. Annual mean clutch-size was positively correlated with field vole abundance in March. The tawny owls used older patches of spruce forest for roosting and nesting. This owl species normally prefers woodland-dwelling species of prey like wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) and as patches of prime field vole habitat in valleys matured to sapling plantations and cutting shifted to upland slopes, where field voles did not occur, the proportion of wood mice and bank voles found in nest remains increased and the territorial population of tawny owls declined (Petty and Fawkes 1997). Thus, in this system, open habitats created by forest management in valleys initially provided another source of food which these tawny owls exploited, but plant succession in these valleys combined with additional manipulation in uplands likely resulted in loss of woodland resources without increasing food supplies.

Potential consequences of the greater use of field voles by the population of tawny owls at Kielder can be seen by comparison with a population at Wytham Wood near Oxford, England. Tawny owls of this latter population roosted and nested within a deciduous (*Quercus-Acer*) woodland and consumed primarily wood mice and bank voles (Southern 1970). Field voles did occur in ungrazed grassy openings and near agricultural enclaves but were consumed at approximately half the rate as the other two prey species. Over a 10-yr period, clutch sizes of tawny owls in Wytham Wood varied 13% around a mean of 2.4 eggs/nest in correspondence with spring abundance of wood mice (Southern

1970), whereas over a 16-yr period, clutch sizes of tawny owls at Kielder varied 20% around a mean of 2.8 eggs/nest in correspondence with fluctuations in abundance of field voles (Petty and Fawkes 1997). Further, the number of territorial pairs at Wytham fluctuated little and grew steadily from 20 pairs in 1949 to 32 pairs in 1959. The number of territorial pairs at Kielder grew from 44 in 1981 to 66 in 1991 then declined to 54 in 1996. This contrast indicates that greater consumption of field voles from populations that fluctuate in multi-annual cycles may lead to higher but more variable reproductive rates and densities of tawny owls.

Because the sizes of alternative and preferred prey described above for tawny owls were similar (~20 g), an example describing relations between the larger Ural owl (*Strix uralensis*) may be more pertinent. In studying a population of Ural owls in cental Sweden, Lundberg (1981) showed that clutch-size was positively correlated with edges between woodland and either newly cleared patches or agricultural fields found within 1 km of the owls' nests. The open habitats supported the owl's two main prey species, the water vole (*Arvicola terrestris*; 100-200 g) and the field vole. The biomass consumed by Ural owls on average included 60% water voles, 14.5% field voles, and 4.9% of mice and other small voles. Field vole populations cycled every 3–4 yrs. Water vole abundance was not sampled, but fluctuations were considered less dynamic and this species was not available until late spring. The owl's courtship and breeding corresponded with the numbers of the smaller prey during spring. Following succession of areas cleared by modern forestry practices, Ural owls shifted their territories as openings proximal to former nest sites became overgrown with dense stands of young conifers. In several cases, owls occupying some territories did not breed for long periods. Lundberg (1981)

attributed the lack of breeding to loss of clearings through succession and the decrease in field vole availability (i.e., diminished access and abundance).

In comparing tawny and Ural owls, Korpimäki (1986) reported that morphology of the talons would suggest use of smaller prey by the former species. He also showed that mean prey weight of breeding-season diets summarized from several studies was smaller for tawny owls ($\bar{x}$ weight = 47.1 g, n = 2,744 items) compared to that for Ural owls ($\bar{x}$ weight = 78.1 g, n = 4,671 items). Korpimäki (1986) also reported that population numbers of the respective species fluctuated 65.7% and 54.1% of the mean number over time. The larger prey weight reported for Ural owls is partially attributed to consumption of the medium-sized water vole, a species with populations that likely do not fluctuate as dynamically as do populations of other voles, which are consumed by both of these owl species (Lundberg 1981, Korpimäki 1986).

Although weather effects were not taken into consideration, patterns from these studies suggest that for forest-dwelling tawny and Ural owls (1) some forms of forest alteration can lead to increases in alternative prey species, which may be consumed in greater amounts than preferred prey and (2) substantial use of prey that undergo greater fluctuations in abundance can lead to greater variation in the owl's reproduction and population numbers.

Long-term studies on spotted owl demography in conjunction with estimates of prey availability have not been published. However, the influence of habitat loss and fragmentation through timber harvest on site occupancy by northern spotted owls and on their demographic responses has been a topic of considerable analysis (e.g., see Meyer et al. 1998, Franklin et al. 2000 and references therein). In general, effects vary according to

extent and pattern of harvesting, regional variation in forest types, and the owl's feeding habits (Carey et al. 1992, Raphael et al. 1996). For example, northern spotted owls dwelling from central Oregon northward into Washington have less access to woodrats and consume greater amounts of flying squirrels (Carey et al. 1992; 1999, Forsman et al. 2001). Clear-cut harvesting removes suitable habitat for flying squirrels, which usually attain greater abundance in late-seral forests (Carey et al. 1992, but see Rosenburg and Anthony 1992). Increased cutting of mature and late-seral coniferous forests in these regions may not only remove spotted owl roosting and nesting habitat, but also diminish a predominant food resource. In addition to flying squirrels, dusky-footed woodrats (*Neotoma fuscipes*) co-occur with spotted owls in southern Oregon and California (Carey et al. 1999, Verner et al. 1992). These woodrats can attain great abundance in early seral stages of mixed-evergreen and redwood (*Sequoia sempervirens*) forest development following clear cut harvesting (Sakai and Noon 1993, Hamm 1995). In northwestern California, northern spotted owls select dusky-footed woodrats over other prey and foraging sites where this prey is more abundant (Ward et al. 1998). Further, unlike the responses described for Mexican spotted owls in the present study, selection of woodrats by northern spotted owls can be linked directly to the owl's reproduction (White 1996, Ward et al. 1998). Accordingly, limited amounts of timber harvesting and habitat fragmentation in these regions may improve the owls reproductive success or overall fitness (Thome et al. 1999, Franklin et al. 2000).

Conservation Goals and Strategies

Conservation strategies for northern and California spotted owls have focused primarily on identifying and protecting optimal arrangements of remaining late-seral

conifer forest from further loss and fragmentation (Thomas et al. 1990, Verner et al. 1992). However, in the Sacramento Mountains, late-seral forests have been replaced extensively by mid-seral conditions but the landscape is also fragmented naturally into patches of plant communities that vary considerably in composition and structure. As the findings here suggest, current conditions are likely associated with elevated variation in the owls' reproductive rate. Hence, simply protecting existing areas from fragmentation is not the most prudent strategy. Rather, a combination of protecting existing roosting and nesting core areas and restoration of late-seral conditions is more appropriate for conserving Mexican spotted owls in this mountain range (USDI 1995).

The structural attributes that distinguish 'old-growth' mixed-conifer forests and that may restore more abundant populations of Mexican woodrats and, ultimately, a more stable population of Mexican spotted owls, could require at least 200 years to develop (Regan 1997). If elevated variation in reproductive rates can be considered a liability to the owl's population persistence, then actions that will provide more immediate increases in availability of Mexican woodrats while also expediting restoration of adequate amounts of mixed-conifer forest to a late-seral condition should be implemented. Further, the current condition of relatively homogeneous, tightly spaced trees with interlocking canopies poses a high risk of extensive stand-replacing fires, which are also a threat to spotted owl persistence (USDI 1995).

Recent demands and plans to thin existing mixed-conifer stands on a landscape scale provide an opportunity for forest restoration. Although the findings presented here support the hypothesis that current forest conditions may have altered the owl's population process, the outcome of future forest manipulation is not without uncertainty.

Careful consideration must be given to designing forest treatments that target enhancement of Mexican woodrat abundance so that responses by this prey species and by Mexican spotted owls can be verified (Block et al. 2001). Below I offer several recommendations that should aid in developing forest-thinning treatments that are proposed to reduce variation in the owl's annual reproductive output.

Experimental Management and Supporting Research

Management actions are usually implemented to solve a particular problem, whereas research is conducted to answer a specific question. In pure form, experimental management does both (Walters 1986). In this instance, the management problem to solve is restoration of forest conditions that reduce risk of fire while concurrently increasing availability of Mexican woodrats to Mexican spotted owls. The corresponding research question is whether or not the implemented treatments are working. In order to answer this question, certain scientific methods must be followed, both during the design phase and during monitoring of selected responses. These include (1) determining the types and extent of treatments to be implemented, (2) determining the response variables to monitor, (3) determining the sampling regime for monitoring response variables, (4) assigning project sites to treatments and controls, and (5) determining operational needs for conducting treatments and monitoring. It is beyond the scope of this Chapter to discuss each of these aspects at length. Others have given thorough consideration to designing monitoring programs that embrace this intent (e.g., Thompson et al. 1998, Block et al. 2001). Rather, a key point to stress here is that without proper design and consideration for monitoring responses, the prediction that proposed habitat manipulations will ultimately enhance conditions for Mexican spotted owls will remain

untested.

Given the findings of this study, two objectives of thinning treatments would be to maximize shrub evenness and to provide suitable log cover for increasing numbers of Mexican woodrats. Concurrent research into the foraging habits of and den site selection by Mexican woodrats would provide useful information for tailoring the objectives of future treatments.

Given the predictions of the working hypothesis, a hierarchy of ecological responses should be monitored to assess treatment effects and refine thinning objectives. At the first tier, Mexican woodrat and deer mouse numbers should be quantified prior to and for several periods after treatments. At a second tier, foraging patterns and food habitats of Mexican spotted owls should be quantified both prior to and following some reasonable time post-treatment to allow for a prey response to be realized. Finally, the most potent answer will come from knowing whether the treatments decreased temporal variation in the owl's reproductive output. This will require several years of monitoring production of spotted owl young. Because trade-offs may exist in the owl's life-history traits, concurrent monitoring of survival and external recruitment is also recommended. In addition, a simulation model may be useful for further exploring the relative influence of habitat succession on the owl's population trends. The most reliable design will entail monitoring of responses of all tiers at treatment and control areas. Ideally, treatment and control areas should be randomly assigned to paired units of area that are similar in character (e.g., elevation and proportions of surrounding vegetation types).

Only by employing key aspects of scientific inquiry to aid design of proposed management actions and to monitor implemented treatments developed from *a priori*

predictions will we come to know the extent of influence habitat alteration has exerted on spotted owls in the Sacramento Mountains. This type of information will be necessary for guiding future restoration of the owl's most limited habitat. It will also permit a more complete understanding of how this predator and its prey respond to various sources of environmental variation.

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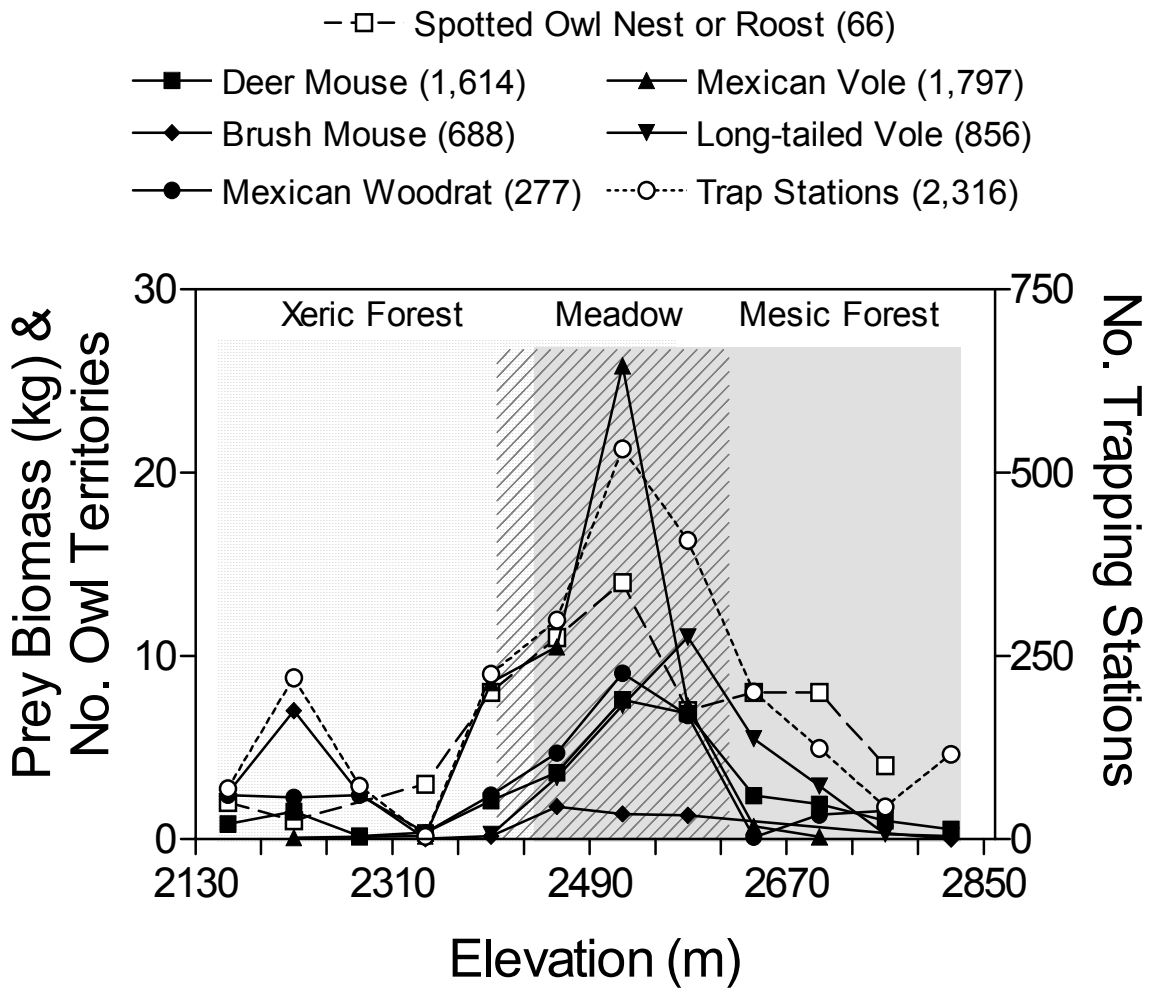

Figure 4.1. Distribution of Mexican spotted owl roost or nest locations and biomass (kg) of five common prey species of the owl by elevation and macrohabitat type in the Sacramento Mountains, New Mexico. Biomass data were collected from randomly selected live-trapping grids during 1992–1996. Elevations were measured at each trapping station of 16 grids. Numbers in the legend indicate the number of spotted owl territories, number of individuals of each rodent species captured and weighed, or the number of trapping stations.

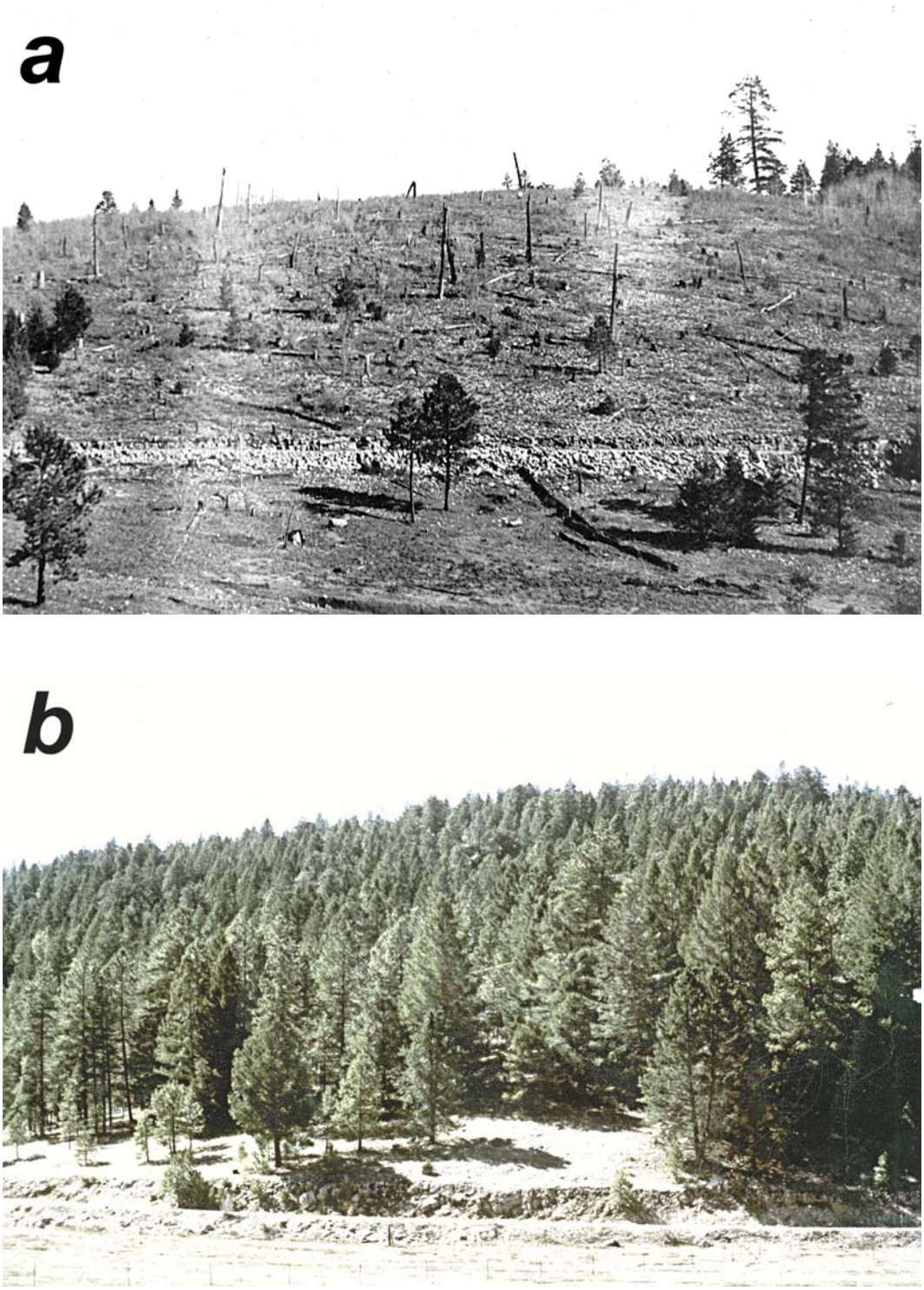

Figure 4.2. One example of forest change in the Sacramento Mountains, New Mexico. This time series photo shows a site in the ponderosa pine zone (*a*) 25 years after clear-cut harvesting in 1903 and (*b*) 92 years after harvest. Photo was taken in Cox Canyon, southeast of Cloudcroft, New Mexico (Lincoln National Forest photo archives).

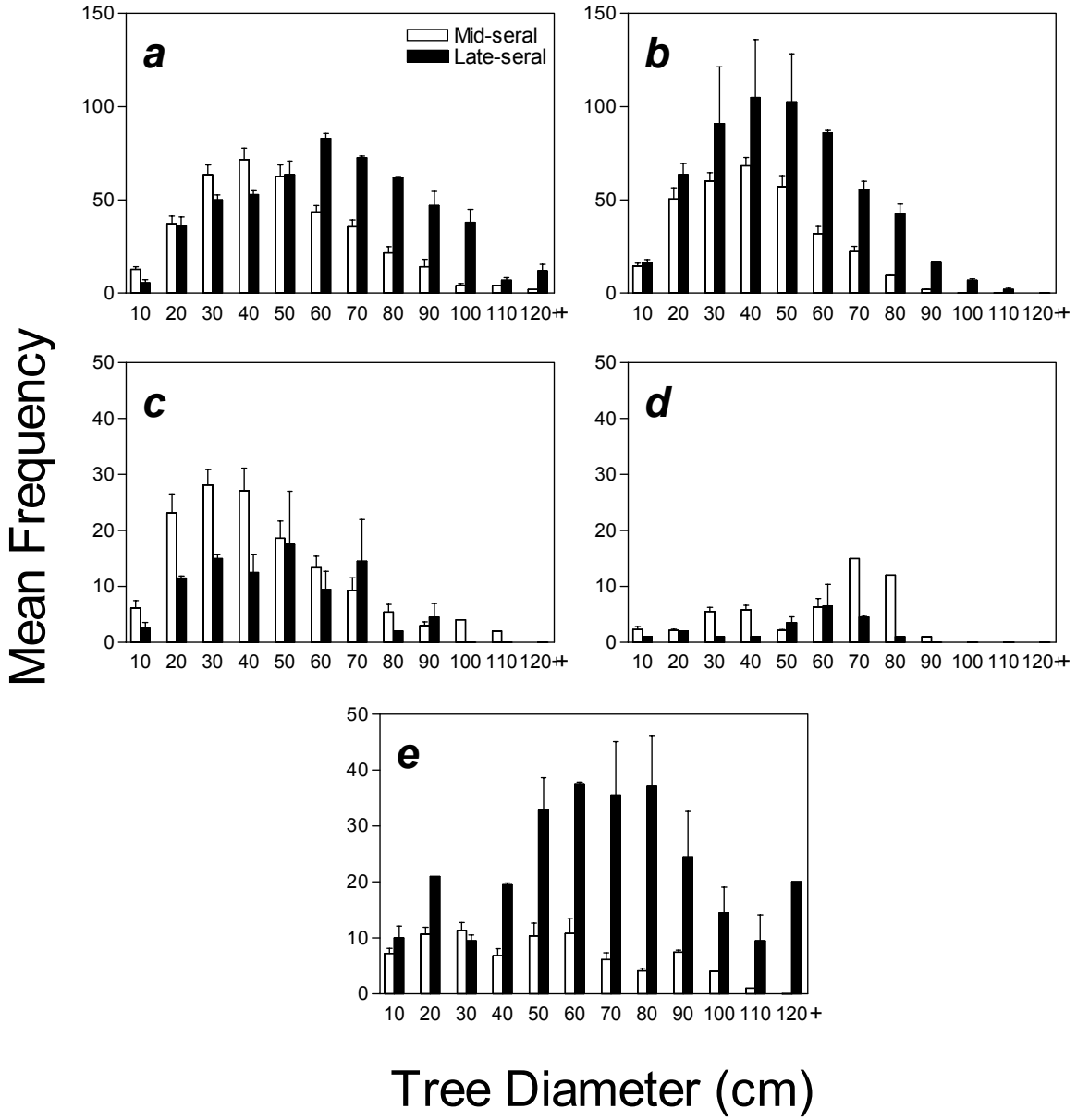

Figure 4.3. Size-distribution of four species of conifers in mid-seral (n = 6, 4-ha grids with 121 tree counts per grid) and late-seral mesic forest (n = 2, 4-ha grids) of the Sacramento Mountains, New Mexico. Live tree distributions are shown for (*a*) Douglas-fir, (*b*) white fir, (*c*) southwestern white pine, and (*d*) ponderosa pine. Distribution of dead trees from each of these species is shown in (*e*). Error bars are one standard error of the mean frequency.

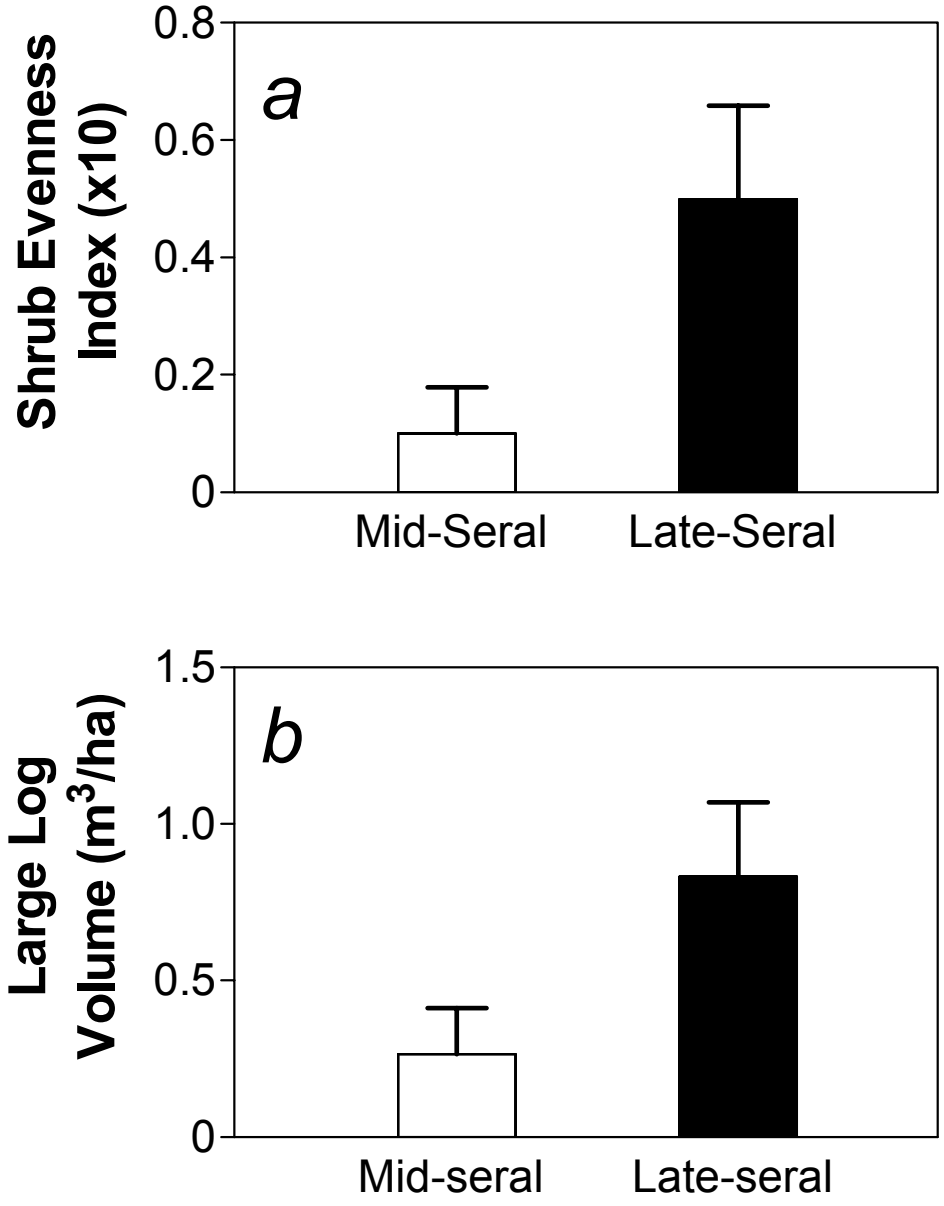

Figure 4.4. Shrub diversity (*a*) and volume of large (>30-cm diameter) logs (*b*) averaged among 121, 78.5-m^2 plots at one mid-seral (60–100 yr) site and at one late-seral (>180 yr) site in mesic forest of the Sacramento Mountains, New Mexico. Error bars are 95% CI. Both microhabitat variables were positively correlated with abundance of Mexican woodrats. Both attributes were significantly greater in the late-seral forest ($P < 0.0001$).

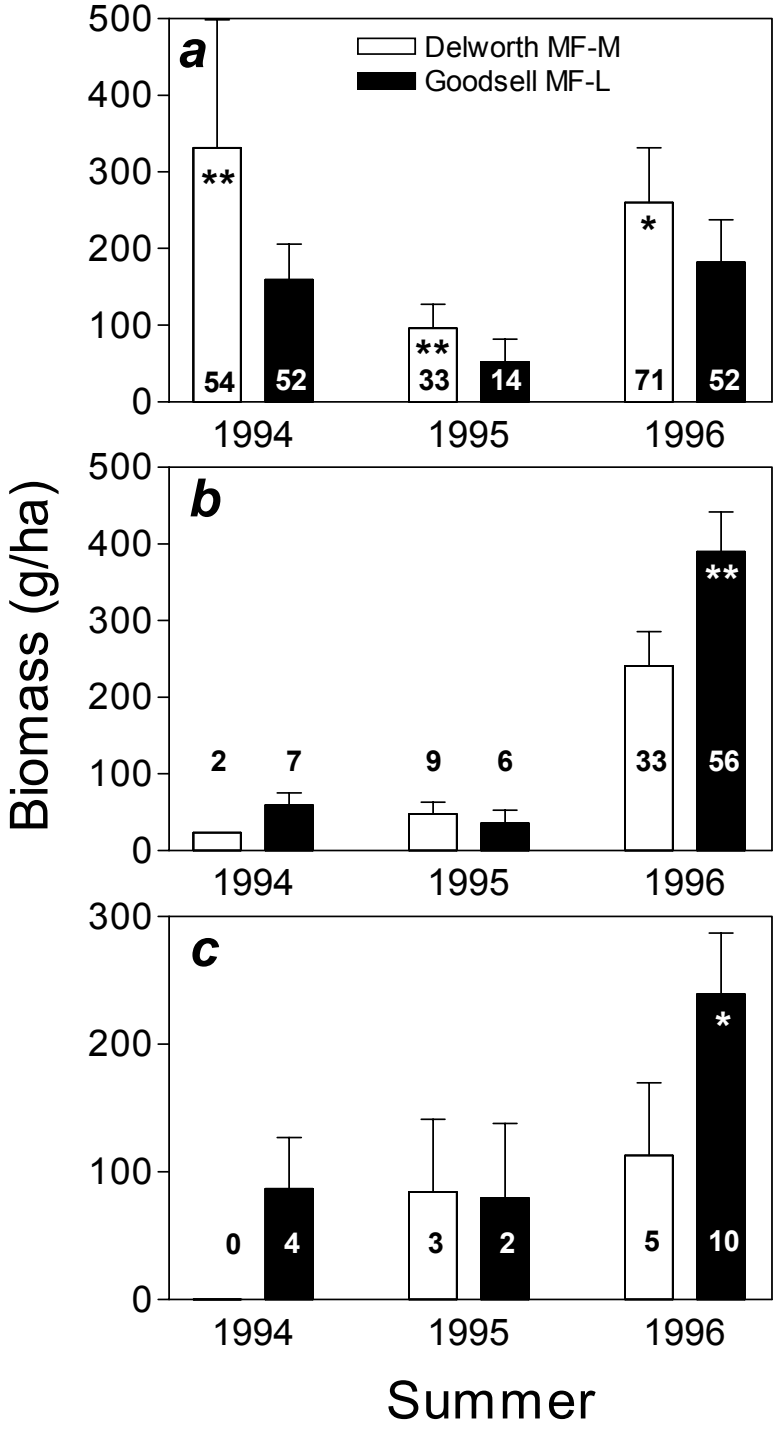

Figure 4.5. Abundance of (*a*) deer mice, (*b*) long-tailed voles, and (*c*) Mexican woodrats at two sites, one in mid-seral (60–100 yrs; MF–M) and one in late-seral (>180 yrs; MF–L) mesic forest during three summers of sampling in the Sacramento Mountains, New Mexico. Standard error bars are enumeration errors. Numbers above or on the bars are number of individuals marked at a site. Asterisks indicate degree of significance of z-test of difference in biomass, * $P < 0.10$; ** $P < 0.05$.

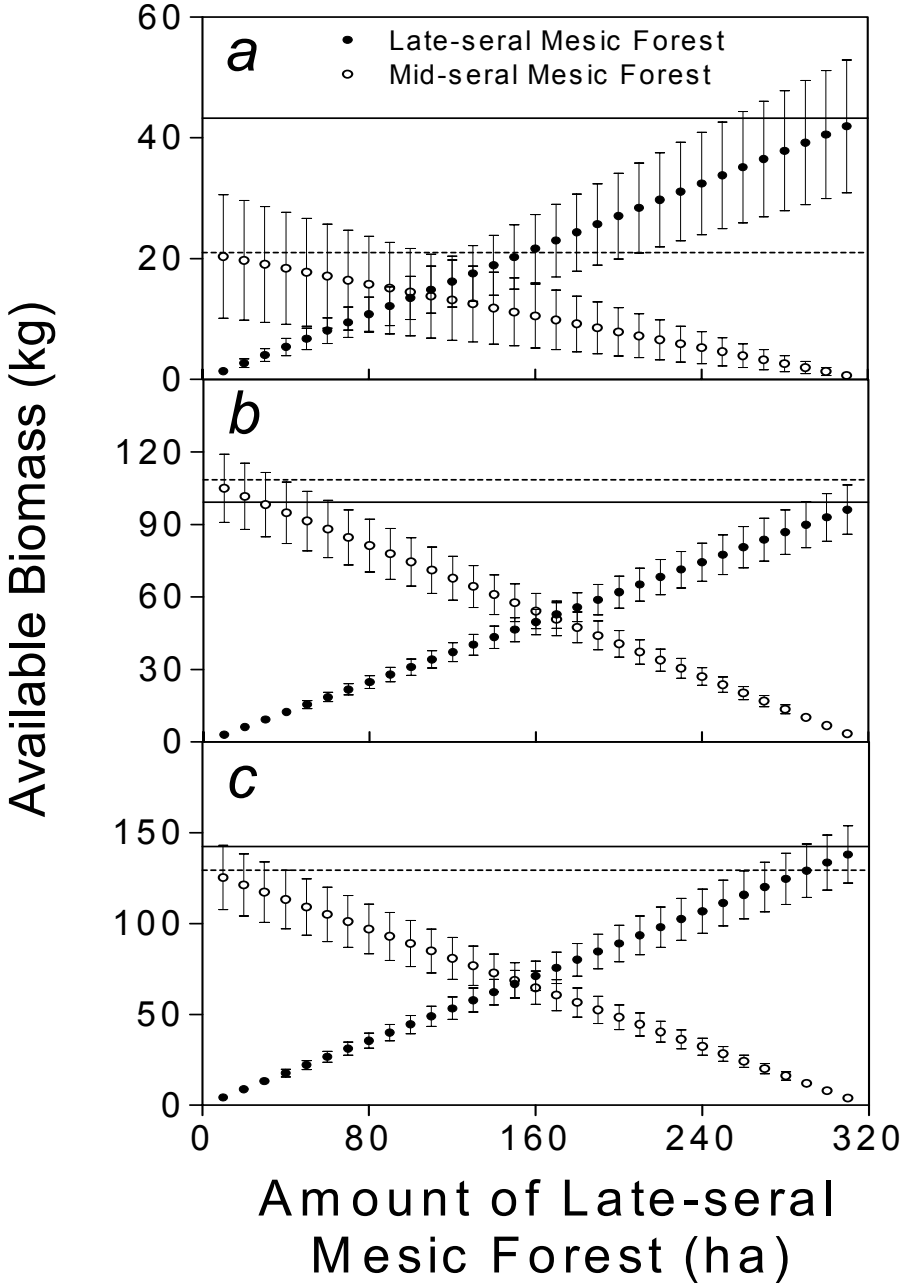

Figure 4.6. Available biomass (kg) of (*a*) Mexican woodrats, (*b*) mice and voles, and (*c*) all five common prey species in two seral stages of mesic forest of the Sacramento Mountains, New Mexico, as a function of habitat area. Estimates are based on three summers (1994–1996) of sampling at one site in both habitats. Error bars are one standard error of the 3-yr mean biomass. Habitat area of mid-seral (60–100 yrs) forest is treated as the additive inverse of late-seral (>180 yrs) forest area. Horizontal lines distinguish average biomass (kg) in 320 ha of late-seral (solid line) or mid-seral (dashed line) mesic forest. The 320-ha area is the amount of mesic forest found in the average-sized home range of a male Mexican spotted owl during the breeding season. Presently, approximately 96% is in a mid-seral stage.

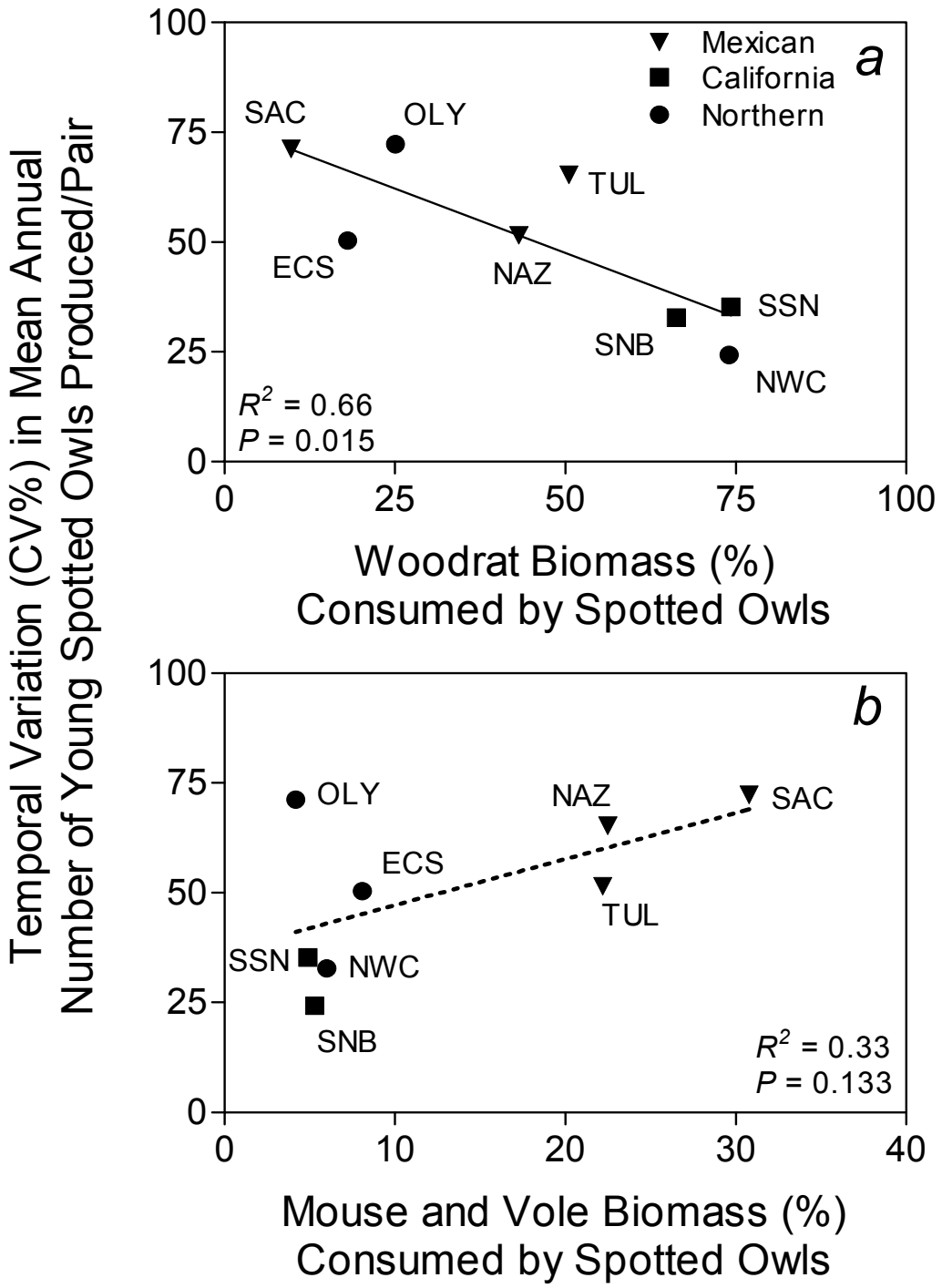

Figure 4.7. Temporal variation in mean annual reproductive output by spotted owls as a function of food habits, estimated as percent biomass of (*a*) woodrats or (b) mice and voles consumed. Data are from eight study areas described in Appendix 4.A and include investigations on all three subspecies. Solid regression line shows a significant relationship (proportion data were arcsin transformed for regression analysis); slope of the dashed line is not significant but is presented to show trend.

APPENDIX 4.A
Sources of Spotted Owl Reproduction and Diet Data

Table 4.A.1. Data from published studies used to assess the relationship between temporal variation in mean annual reproductive output (number of young/pair) by spotted owls ($CV_t\ [\bar{\bar{RO}}]$) and consumption of woodrats or mice and voles during the breeding season. Asterisks indicate studies reporting female fecundity which was converted to reproductive output as (fecundity•2).

	Number of Young Found Per Pair						Prey Biomass (%) Consumed					
Subspecies / Study[a]	Years	Number[b] of Pairs	Temporal[c] Variance	Mean[d]	$CV_t[\bar{\bar{RO}}]$ %[e]	Source	Years	Sites	Owl Items	Prey rat[f]	Wood- and Vole	Mouse[g] Source
Mexican												
SAC	1991–96	19–51	0.2732	0.72	72.3	Present study	1991–96	36	2138	25.1	30.8	Present study
TUL	1991–95	18–26	0.3036	0.84	65.3	Seamans et al. 1999*; Gutiérrez et al. 2001	1991–95	41	2162	50.5	22.5	Seamans and Gutiérrez 1999
NAZ	1991–95	18–31	0.3192	1.10	51.6	Seamans et al. 1999*; Gutiérrez et al. 2001	1991–95	44	1631	43.2	22.2	Seamans and Gutiérrez 1999
California												
SNB	1987–91	31–86	0.0164	0.53	24.3	LaHaye et al. 1994; (pers. comm.)	1987–91	109	8169	74.0	5.3	Smith et al. 1999
SSN	1990–94	~16	0.1135	0.95	35.3	North et al. 2000	1988–92	11	278	74.3	4.9	Munton et al. 1997
Northern												
NWC	1987–94	65–76	0.0417	0.62	32.8	Franklin et al. 1996; Franklin et al. 2000	1987–95	63	672	66.3	6.0	White 1996
ECS	1989–93	~96	0.4348	1.31	50.4	Forsman et al. 1996*	1983–96	34	1867	18.1	8.1	Forsman et al. 2001
OLY	1987–93	~278	0.2324	0.68	71.2	Forsman et al. 1996*	1983–96	151	4238	9.8	4.2	Forsman et al. 2001

Table 4.A.1. (Continued).

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[a] SAC—Sacramento Mountains, New Mexico; TLM—Tularosa Mountains, New Mexico; NAZ—Northern Arizona; SNB—San Bernardino Mountains, California; SSN—Southern Sierra Nevada, California; NWC—Northwestern California; ECS—Eastern Slope of Cascade Range, Washington; OLY—Olympic Penninsula, Washington.

[b] Range indicates minimum number of owl pairs checked in a year to the maximum number checked; ~ indicates annual numbers of pairs not given in sources, only total territories in oak woodland type (SSN) or total number of females ≥3 yrs (ECS, OLY).

[c] Temporal variance estimated as total variance − mean sampling variance. The latter was estimated as the average among sampling variances for each annual estimate of mean number of young produced per pair.

[d] Averaged among all years in the study.

[e] Estimated as the square-root of temporal variance divided by the mean.

[f] Includes *Neotoma mexicana*, *N. albigula*, *N. fuscipes*, and *N. cinerea*.

[g] Includes members of the genera *Peromyscus*, *Microtus*, *Phenacomys*, and *Clethrionomys*.