The Role of Urban Forests in Conserving and Restoring Biological Diversity in the Lake Tahoe Basin

Draft Final Report

January 22, 2007

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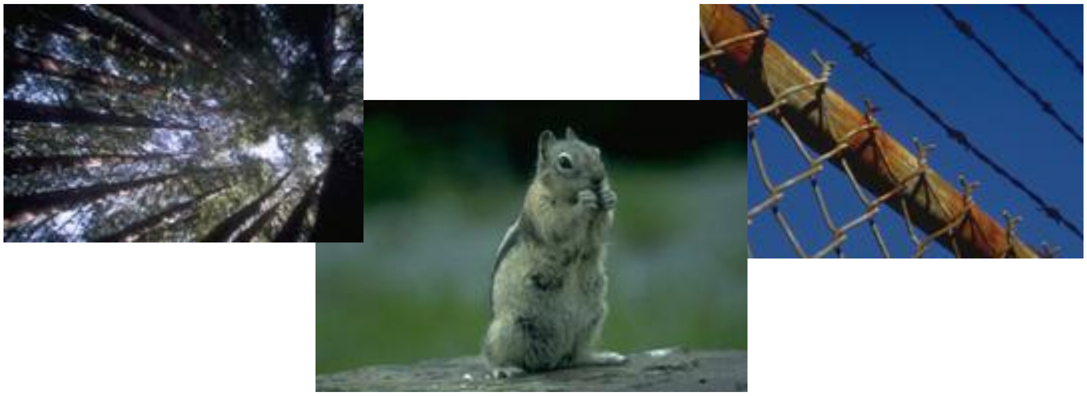

In compliance with
CCA 01-CS-11051900-022
(SNPLMA Funding)
submitted to:

USFS Lake Tahoe Basin Management Unit
Tahoe Regional Planning Agency
Nevada Division of State Lands

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Executive Summary

Introduction and Methods

Multiple state and federal agencies in the basin have land acquisition programs that purchase parcels of land that are sensitive to management or serve important ecological services, such as wetland areas in residential or commercial zones or flood plain areas in sensitive watersheds. The U.S. Forest Service manages the greatest acreage of urban forests of any agency in the basin, 5200 ha (13,000 ac) of land in 3500 separate parcels, for an average parcel size of 1.5 ha (3.7 ac). In 2002, we started this study to evaluate the contribution of urban forests to supporting biological diversity in the Lake Tahoe basin. The project was collaboratively funded by the USFS Lake Tahoe Basin Management Unit, University of Nevada Reno, USFS Sierra Nevada Research Center, Tahoe Regional Planning Agency, and Nevada Division of State Lands. An 8-person science team was assembled to accomplish the task, which consists of Forest Service scientists, University professors, and graduate students.

This final report summarizes the activities and results of the entire study. Five taxonomic groups were investigated: birds, small mammals, large mammals, ants, and plants. A sampling frame was developed based on development within a 300-m radius of a given site. The number of site sampled for each taxonomic group ranged from 70 to 130 sites, with approximately 60 sites sampled for all taxa. Sites were located all around the Lake Tahoe basin. The level of development at sample sites ranged from no development within 500 m to nearly 80% developed within 300 m.

Many sampling methods were employed over the three-year period of data collection (2003-2005). Bird species composition, density, reproductive success, and behavioral patterns of passerines were characterized over a three-year period at a total of 75 sites with three techniques: point counts (75 sites), nest monitoring (97 sites), and behavioral observations (75 sites). Sciurid populations were sampled over a three-year period using Sherman live trap grids (64 traps) at 65 sites, 25 of which were sampled each of three consecutive years. Medium- to large-bodied mammals were surveyed over a two-year period (2003-2004) at a total of 77 sites using track and photographic surveys (four track plate boxes and two cameras), and pellet-group counts (for deer and leporids). Ground-dwelling ants were sampled over a two-year period (2003-2004) at a total of 120 sites using pit-fall trap grids (12 traps). Plant populations were characterized over a two-year period (2003-2004) at 100 sites with a variety of sampling methods, including fixed plots, quadrats, and line intercepts to characterize plant species composition and structure. Human use of the sites was characterized in 2003 and 2004 terms of the types, intensity, and spatial and temporal distribution of anthropogenic disturbance by conducting visual encounter surveys along transects at the same 100 sites sampled for plants. Preliminary results indicate a variety of positive and negative relationships between development and the composition and abundance of plant and animal species.

Results

Human Use

The number of people detected per site ranged from 0 to 11 people per hour, with the exception of one site with over 30 people/hr. Use by people varied depending on the month, time of day, and time of week. Use peaked in July, followed by August and June. Use was greatest on the weekends, and it was heavier in the afternoon and evening than in the morning. This indicates that summer visitors comprise a large proportion of users of these urban forest parcels, which is perhaps a new perspective on how many visitors spend their time and what aspects of land management in the basin will affect visitor satisfaction. The greater level of use in the latter portion of the day is consistent with the idea that most people go for walks with or without pets toward the end of the day. Dogs were detected on over half of the sample sites. The number of dogs detected per hour per site ranged from 0 to 4.5, with 72% being unrestrained. Dogs were more likely to be restrained in more developed areas.

Human use was positively related to development within 300 m of the site center, and the number of vehicles showed an even stronger positive relationship with 300-m development. So, although use was positively related to development, it was clear that some sites with low development received high use, particularly non-motorized use. Further, it appears that some types of impacts from dogs (e.g., wildlife harassment and mortality) can be as great or greater in less developed areas because a greater proportion of dogs are unrestrained.

Birds

We conducted point counts 75 sample sites that spanned the development gradient. We detected 67 native landbird species, excluding waterbirds and raptors. Species richness ranged from 5 to 28 species and abundance ranged 5.3 to 59.0 individuals. We located and monitored nests in these sites and an additional 22 sites for a total of 97 sites. A total of 570 nests were discovered and monitored.

Landbird community structure changed substantially along the development gradient. This change was driven by multiple species, primarily those more frequently occurring at either the low or high end of the gradient. Species making the largest contribution to the differences in composition among development categories were Brewer’s Blackbird (more prevalent at more developed sites), Dusky Flycatcher, White-breasted Nuthatch, Hermit Thrush, and Cassin’s Vireo (all more prevalent at less developed sites). Landbird species richness declined steadily with increasing development; we did not find the peak in diversity at moderate development that some other studies have found. We did not see a strong pattern of association between total bird abundance and development or human use, but over half the landbird species were negatively or positively associated with development. Human use was consistently more important in explaining abundance of species groups than was percent development. Ground nesters were most associated with landscape-level vegetation, specifically conifer forest and aspen-riparian ecosystems, as opposed to development. Cavity nesters were most associated with local vegetation structure, especially snag volume. Ground-foraging omnivores were most associated with human use, which likely brings an increase in food resources for these birds. Invertivores were associated with local vegetation structure specifically high snag volume, high canopy cover, and low tree density.

The success of nests (probability of fledging at least one young) also was affected by development based on over 500 monitored nests. Nest success was high for cavity nesters and considerably lower for open nesters, whose success was lower with increased development. Among open nesters, shrub and ground nesters fared worse than tree nesters. Nest success also declined with development for three of the 10 individual bird species examined (Dark-eyed junco, Pygmy nuthatch, and Western wood-pewee), and many other common species simply did not nest in urban forests.

Small Mammals

From 2003-2005, over 31,000 trap nights resulted in the capture of 6,400 individuals and 19 species. Total species richness averaged 5.3 species per site (range = 2 to 9), and species richness for squirrels and chipmunks averaged 4 species per site. On average over 95% of individuals captured were squirrels and chipmunks. Community composition was significantly influenced by development based on multiple response permutation procedure (MRPP) analysis; there was a significant difference in species composition between sites with low (1-10%) and high (>10%) development. The species that most influenced compositional heterogeneity were voles, Golden-mantled ground squirrels and Deer mice.

Multiple regression analysis and the model selection procedure identified important factors that influence small mammal species richness and relative abundance in the Lake Tahoe basin. Development had a limited effect on small mammal richness and abundance; there was a weak positive relationship with development, and stronger positive associations with the amount of bare ground, sampling year, and habitat heterogeneity, and negative associations with Julian sampling date, other ground cover substrates, and volume of coarse woody debris.

Patterns of abundance and population dynamics of individual squirrel and chipmunk species showed stronger relationships with development and human disturbance than community metrics. Long-eared chipmunks were the most numerous and evenly distributed of all the small mammal species sampled. Development at the 1000m spatial scale influenced survival, but the decrease in survival with increasing development was less pronounced than the year effect. Emigration rates increased with development. Survival in yellow-pine chipmunks was negatively influenced by development and disturbance, as well as group affiliation and sampling year. Development at the 300m scale had a pronounced negative impact on adult survival in yellow-pine chipmunks, as did disturbance in the form of frequency of dogs at the site. Sampling year was the most important factor affecting survival, but development at the 1000m scale and disturbance also affected survival (Table 3.20). Similarly, survival rates of lodgepole chipmunk were negatively affected by both development and disturbance. In contrast, while development had a negative effect on survival of shadow chipmunk, disturbance in the form of dog and human use appeared to positively affect their survival.

For California ground squirrels and golden-mantled ground squirrel, development had a significant negative impact on survival, and emigration was facilitated by development in golden-mantled ground squirrels. Development at the 300m and 1000m scales also negatively affected Douglas squirrel survival rates.

We identified several important explanatory factors that influence small mammal species richness and abundance in the Lake Tahoe basin. Habitat variables such as percent cover of bare ground and overall habitat heterogeneity positively affected both small mammal species richness and abundance; however, urban development and associated disturbance were also found to impact richness and abundance. While the patterns of species richness and relative abundance we found do not reflect highly negative effects of urbanization, the negative relationships we did observe suggest that further development will have increasingly negative effects on small mammal populations, particularly the more vulnerable species such as shadow chipmunks and lodgepole chipmunks. As development expands, natural habitat patches decrease in area and survival is expected to decline, most likely resulting in a more pronounced change in the richness and abundance of small mammal species.

Large Mammals

Large mammals were sampled at 86 sample sites across the development gradient. Ten carnivores were detected: eight native species, and the domestic dog and cat; in addition, rabbits, hares, and deer were detected. Domestic dogs were the most commonly detected species at a sample unit, and they were recorded at 64% of sites. Coyote, black bear, raccoon, and rabbits and hares were each detected at ≥40 % of sample units. The least commonly detected species were bobcat, weasels, and spotted skunk. Species richness (1 to 6 species) did not differ significantly along the development gradient. Martens and skunks showed a skewed distribution being detected at only those sites where development was < 30%, and black bear showed a negative relationship with development. Coyotes were relatively evenly distributed across development classes. Martens dominated detections at the least developed sites (<1 % developed), accounting for 48% of detections, whereas domestic dogs accounted for the majority of detections in all other development categories. Community composition analysis reflected these basic relationships in that composition was significantly different among three development categories, with marten being the primary native species responsible for changes in composition along the gradient.

Species richness and occurrence were influenced by a variety of environmental features, including development. Carnivore richness was most closely associated with microhabitat characteristics, specifically the volume of coarse woody debris, and the density of large and small trees, whereas herbivore richness was equivalently related to many environmental variables and not well predicted overall. Predictably, the two non-native species, domestic dog and cat, were strongly associated with anthropogenic influences. Models containing development and anthropogenic characteristics also performed well to describe the occurrence of coyote and raccoon, the two native carnivore species considered to be tolerant of human presence and activity. Two native species, marten and black bear, were less strongly associated with anthropogenic influences. The best model for marten occurrence was a combined model of human activity and total snag density, and the best model for black bear occurrence was comprised of macrohabitat composition variables. Development also appeared to affect behavior, as reflected in the time of day sites were visited. Raccoons were active primarily at night but appeared to be active more frequently during daylight hours at more developed sites. Dogs were generally detected during daylight hours. In contrast, coyotes were generally detected after dusk (after 2000 hours) and before dawn (before 0600 hours), but were detected more frequently during the day at less developed sample units. Similarly, black bear exhibited strong nocturnal behavior at sample units with moderate to high levels of development, whereas bears were active during all time periods at less developed sites.

Ants

A total of 32,023 individuals from 46 species were recorded from the 101 sites sampled. Site species richness ranged from 3 to 20 species, and abundance was a strongly correlated with species richness. Ant abundance was not significantly correlated with percent development at any scale. Conversely, species richness increased across the gradient at the 300-m, 500-m, and 1000-m scales, and peaked at intermediate levels of development within 100 m. The only species group that showed a significant relationship between abundance and the development gradient was the frequency of rare species, which declined with increasing development, and few rare species were found above 60% development.

Eight species were either negatively or positively affected by development at various scales, with the 60-m scale appearing to have the greatest effect. We found that the 60-m scale on average explained an increasingly greater proportion of the variation compared to increasing radii around the site. Five species were negatively and one positively associated with 60-m scale of development.

At small scales, disturbance also appeared to affect ant species richness and abundance. Species richness declined significantly as the total area of compacted surface increased within 30 m. Species richness and abundance declined in proximity to (30 m) highways, OHV, and residential developments. Ant richness peaked at moderate levels of site-specific (within trapping grids) disturbances. Species richness differed significantly between ranked disturbance classes, with species richness in moderately disturbed sites being 25% greater than in low disturbance sites and 10% greater than in high disturbance sites. Ant abundance was greatest in the moderate disturbance class, but did not vary significantly across disturbance classes.

Plants

Native vegetation was not greatly altered in native forests in response to increasing surrounding development. Total species richness increased slightly with development, primarily due to increased numbers of exotic annual and perennial herb and grass species. Urban development did not appear to impact percent cover of native annual herbs, perennial herbs, and shrubs; however, in the larger landscape, shrub cover did decline with development. In native forests, surrounding urban development also had no impact on tree species composition, density, basal area, or number of canopy layers.

However, canopy cover did decline in the larger landscape, and showed a slight decline in native forest sites, suggesting that native forests provide higher canopy cover conditions than would otherwise occur in developed areas, but it may be compromised relative to undeveloped conditions. The diversity of height classes occupied by vegetation was not correlated with development. Decadence features showed no obvious correlations with environmental factors, but only because disease was prevalent along the entire development gradient. Urban development was strongly associated with the loss of woody debris from the ecosystem regardless of the type of site (native forest or larger landscape). Snag density, snag volume, and volume of coarse woody debris were negatively correlated with development, while number of cut stumps was positively correlated. While remote sites varied greatly in amount of dead wood, highly developed areas had consistently low dead wood densities. Average snag decay class also declined with development.

Landscape Model (to be developed)

Chapter 1: Introduction

Background

This study was initiated in 2002 to evaluate the contribution of urban forests to supporting biological diversity in the Lake Tahoe basin. The study was collaboratively funded by the USFS Lake Tahoe Basin Management Unit, University of Nevada Reno, Tahoe Regional Planning Agency, USFS Sierra Nevada Research Center, and Nevada Division of State Lands. The study investigated the effects of urbanization and human disturbance on landbirds, small mammals, large mammals, ants, and plants. The project was initiated to develop inferences about the contribution that parcels of native forest (i.e., undeveloped parcels) make to supporting wildlife populations and biological diversity in these more urban settings. Parcels of National Forest System lands were of particular interest. Previous reports and other project-associated products can be obtained from the Lake Tahoe Basin Management Unit or from the authors of this report.

The science team consisted of Forest Service scientists and University professors and doctoral students from the Sierra Nevada Research Center of the Pacific Southwest Research Station, University of Nevada at Reno, and University of California at Davis (Table 1.1). The diversity of team members brings a great depth and breadth of expertise to the study, including invaluable ecological insights from a long history of working in the Lake Tahoe basin and the Sierra Nevada.

Table 1.1. Science team for the Lake Tahoe Urban Biodiversity project.

PSW Sierra Nevada Research Center	**University of Nevada, Reno**	**University of California, Davis**
Pat Manley – PI	Dennis Murphy – PI	Matt Schlesinger – landbirds
Lori Campbell – large mammals	Susan Merideth – small mammals	Kirsten Heckmann – plant species and communities
Sean Parks – GIS	Monte Sanford – ants	Marcel Holyoak – advisor
	Peter Brussard – advisor	Michael Barbour – advisor

Scientific Foundation

The Lake Tahoe basin is particularly vulnerable to the loss of biological diversity because of its physiognomy and geographic location (Manley et al. 2000). Lake Tahoe is located in a small and topographically isolated montane basin with a steep elevational gradient that serves to create a high level of natural habitat fragmentation. Ecological assemblages within the basin are also naturally fragmented; the steep elevational gradient of the basin, combined with its location in a transition area between the Great Basin and Sierra Nevada zoogeographic regions (Udvardy 1969), result in a high diversity of vegetation communities and associated plant and animal species. The Lake Tahoe basin also provides an ideal opportunity to further our understanding of fragmentation and human disturbance effects on biological diversity.

Multiple state and federal agencies in the basin have land acquisition programs that purchase parcels of land that are sensitive to management or serve important ecological services, such as wetland areas in residential or commercial zones or flood plain areas in sensitive watersheds. The U.S. Forest Service manages the greatest acreage of urban forests of any agency in the basin, 5200 ha (13,000 ac) of land in 3500 separate parcels, for an average parcel size of 1.5 ha (3.7 ac). In contrast, the California Tahoe Conservancy manages 30% more parcels than the U.S. Forest Service, but a lower total area of land, 2540 ha (6350 ac), for a smaller average parcel size of 0.6 ha (1.4 ac). Nevada Division of State Lands also manages urban forest parcels in the basin, but at a small scale compared to the other two agencies, with only 500 parcels and 100 ha (250 ac) of land area. These parcels are distributed all around the basin, but are most prevalent in the southern portion of the basin and at lower elevations.

In 2001, Congress questioned the benefits of the U.S. Forest Service lands acquisition through the Santini-Burton program, given its high cost and the urban setting of many of the parcels. The location and size of parcels acquired through the Santini-Burton program vary widely, from 0.2 ha to hundreds of hectares, with the majority of parcels being 1ha or less. Congress requested an evaluation of the value of these “urban lots” in the Lake Tahoe basin in meeting agency objectives, such as water quality, biological diversity, and recreation. The future of the Forest Service’s land acquisition program will be shaped in part by the outcome of the evaluation. A study of the landscape geometry, and specifically the contribution of undeveloped parcels located in the more highly developed lower elevation areas in the basin, was needed to provide the necessary information to respond to Congress and to inform land acquisition and management programs in the basin.

A project to evaluate the contribution of urban forests to supporting biological diversity in the Lake Tahoe basin was initiated and collaboratively funded in 2002 by the USFS Lake Tahoe Basin Management Unit, University of Nevada Reno, USFS Sierra Nevada Research Center, and Tahoe Regional Planning Agency. The results of the project will be used to make inferences about the contribution that parcels purchased through the Santini-Burton project contribute to supporting biological diversity in the basin, and the contribution that parcels in the urban forests (i.e., undeveloped parcels of any affiliation) make to supporting wildlife populations and biological diversity in these more urban settings. The “Lake Tahoe Urban Biodiversity” project completed its first season of field data collection during the spring and summer of 2003. The activities conducted and accomplishments achieved to date are described in this report, as well as plans for the 2004 field season. More detailed information on study objectives and methods can be found in the full study plan on the Sierra Nevada Research Center web site (www.fs.fed.us/psw/programs/research_emphasis_areas/ecosystem.currentstudies/landscape_watershed/pattern_landscape_laketahoe/shtml).

The effects of fragmentation and disturbance on population and community dynamics in the Lake Tahoe basin are not well known. Species restricted to lower elevations are most vulnerable given that development, and therefore disturbance and fragmentation, is greatest at lower elevations (e.g., Manley 2000, Manley and Schlesinger

2001). Many data gaps and uncertainties exist – the objectives of this study were to describe changes in biological diversity in relation to development and associated human use, address key hypotheses about causal linkages, identify potential indicators of declines of biological diversity in response to human development, and identify potential thresholds for maintaining biological diversity at the parcel and basin scales. Species respond uniquely to development and associated disturbance, so we sampled a wide array of taxa. Vulnerabilities and predicted effects of development and disturbance associated with each taxonomic group studies are outlined below.

Objectives

The study was designed to inform three basic management activities and needs: development, assessment, and management. The primary objective of the study was to evaluate effects of loss through development, however in the course of this objective, potential indicators of biological integrity will emerge that can be useful for assessment. Although the study was not designed to directly address the effects of management activities (e.g., vegetation management), site conditions that have a relatively strong effect on its capacity to achieve its biological potential can be inform management. In the initial project description, these three management activities were represented by the following specific management objectives.

Development

1. How does anthropogenic disturbance within and around urban lots affect the ability of urban lots to support their native diversity of species? What management options exist for reducing the negative effects of disturbance?
2. What role do urban lots play in supporting biological integrity at the landscape scale? How might that role shift in light of various development (i.e., build-out) scenarios within the basin?
3. What are the predicted effects of various patch and landscape-scale management scenarios regarding urban lot management (i.e., development, acquisition, restoration)?

Assessment

4. What are reliable criteria for identifying potential indicator species?
5. Do particular species, species groups, or environmental parameters emerge as strong indicators of biological integrity at the patch or landscape scales?

Management

6. What management options exist for improving the biological integrity of existing urban lots?

In pursuit of rigorous scientific investigation, these management objectives were translated into scientific objectives, which then shaped the design of the study.

Development

1. Do thresholds in the persistence of individual species, composition of species assemblages, character of species interactions, and species richness exist at the forest stand scale along fragmentation and disturbance gradients?
2. Does species composition across stands exhibit a nested structure, such that less species-rich stands are generally occupied by more frequently occurring species?
3. Has the basin exceeded a fragmentation threshold such that habitat loss now has a greater impact on biological diversity than would be expected based on area losses alone (i.e., shifted from the random sample model to a metapopulation model)?
4. Is the fragmentation threshold lower than expected as a result of natural fragmentation within the basin?
5. Does anthropogenic disturbance (historic, recent, chronic) interact with fragmentation to reduce or otherwise shift thresholds of integrity/degradation at stand and landscape scales? At the patch scale, does this interaction vary in association with other environmental factors such as vegetation type, elevation, orientation, or the type of anthropogenic disturbance?

Assessment

6. Are there particular species or species groups that appear to be more sensitive to fragmentation and/or disturbance (i.e., shifts in condition observed for some species at lower levels of fragmentation or disturbance compared to others)?
7. Are species or groups of species predicted to be strong indicators of biological integrity based on theories of community ecology substantiated or are they refutable based on empirical data?

Management

8. What environmental parameters best predict patterns of stand-scale species occupancy and reproductive success, composition and richness?

Study Area and the Development Gradient

The study area is the Lake Tahoe basin, a physically and biologically unique feature in between the flanks of the Sierra Nevada range of California to the west and the Carson Range of Nevada to the east (Fig. 1.1).

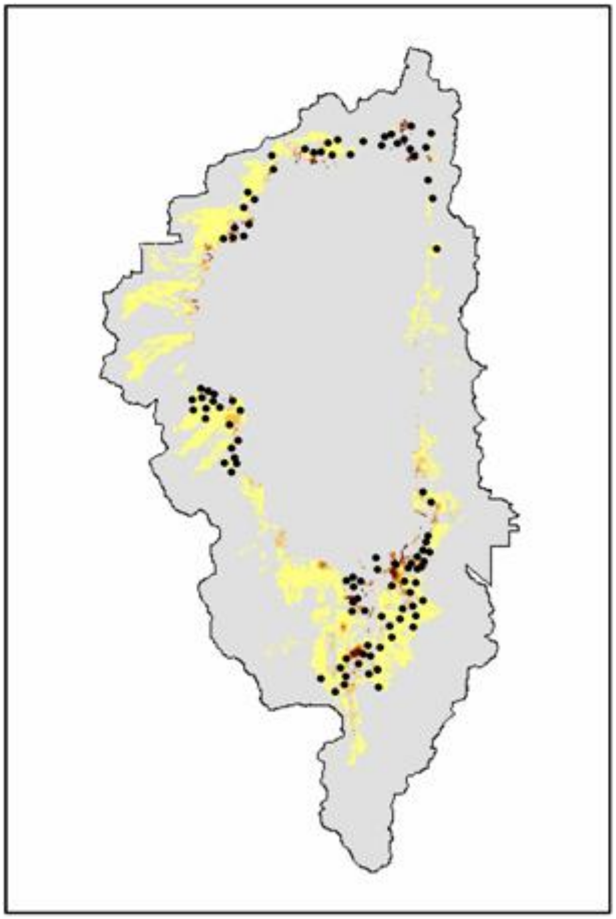


Figure 1.1. Sample site locations (n ≈ 100) around the Lake Tahoe basin.

The Lake Tahoe Basin is located high in the central Sierra Nevada (38.90° N and 120.00°) and spans the border between California and Nevada. Flanked by the Sierra Nevada in the west and Carson Range in the east, the basin includes both Lake Tahoe, having a surface area of 49,000 ha, and its surrounding watershed, 82,000 ha (Barbour et al. 2002). Elevation ranges from 1,900 m a.s.l. at lake level to 3,050 m at the highest peak (Elliot-Fisk et al. 1996).

A strong precipitation gradient exists from west to east, such that the Tahoe Basin encompasses two very different climate regimes. Average annual precipitation in the northeast shore is about half that of the southwest shore (James 1971). Two-thirds of the annual precipitation falls from December to March, more than 80% of which falls as snow. The winter mean daily minimum temperature at lake elevation is about -6° C, while the summer mean daily temperature exceeds 30° C (Manley et al. 2000).

The basin contains three main vegetation zones: lower montane (lake level to 2,200 m a.s.l.), upper montane (2,200 to 2,600 m a.s.l.), and subalpine (>2,600 m a.s.l.). This project was restricted to elevations between 1,920 m (lake surface) and 2,134 m, which falls within the lower montane zone, because it contains roughly 95 percent of the urban area in the basin (TRPA 2002). The most common lower montane forest types are Jeffery pine, mixed-conifer, and white fir (Manley et al. 2000). In addition, lodgepole pine (*Pinus contorta*) dominated forest is found in moist habitats throughout the basin and a mix of alder (*Alnus* spp.), willow (*Salix* spp.), and aspen (*Populus tremuloides*) is common in riparian areas.

A very limited amount of virgin forest exists in the Tahoe Basin today due to intensive logging during the nineteenth century. Remnants of original forest exist throughout the basin, primarily at higher elevations on the west side (Bailey 1974). Barbour et al. (2002) located and described 38 remnant old-growth patches in the Tahoe Basin. Core sample sites were selected using a development index as the sampling frame. The development index was developed through a number of steps (see Parks et al. *in review*).

First, we created a single transportation GIS layer for the basin by combining several transportation GIS data layers provided by the LTBMU, California State Parks, and the Nevada Division of State Parks. To give the transportation features area, we buffered each transportation feature based on the type of transportation feature it happened to be. Highways were buffered 6.9 m (for a total width of 13.8 m), regular paved surface streets were buffered 5.1 m (10.2 m wide), dirt roads were buffered 3.3 m (6.6 m wide) and trails were buffered 0.5 m (1 m wide). The buffering distance was based on the basic width of a traffic lane, the average width of the shoulder (both of these values from the CalTrans highway design manual) and the average number of lanes. The buffered transportation features were then converted to a grid with a pixel size of 3 by 3 m.

Second, a land-use type was assigned to each parcel within the basin using a land-use GIS layer obtained from the Tahoe Regional Planning Agency. Examples of land-use types include: single family dwelling, hotel/motel, service station and animal husbandry services. There were a total of 60,137 parcels within the basin representing 90 different land-use types, so the land-use GIS layer was extremely detailed.

Third, we estimated the proportion of developed land for each land-use type by taking a random selection of parcels from each land-use, and then estimating the proportion of developed land using digital orthographic quadrangles. For land-use types with more than 200 parcels, we randomly selected 30 parcels and estimated the proportion that was developed in each parcel; for land-use types with 51 to 200 parcels, we randomly selected 20 parcels; for land-use types with 10 to 50 parcels, we randomly selected 10 parcels; and for land-use types with less than 10 parcels, we selected all parcels. For each land-use type, we averaged the estimated percent development for all the randomly selected parcels. For instance, the average proportion developed for single family dwelling was 51%.

Fourth, we converted the land-use layer into a grid with a pixel size of 3 by 3 m. For each land-use type, a proportion of the cells were reclassified into a developed category. For example, in areas where single family dwelling was the land-use, 51% of the 3 m^2 pixels in those areas were assigned a value of 1 (developed = 1, non-developed = 0). This was performed on each land-use type in the basin.

Fifth, the land-use GIS grid and the transportation GIS grid, both with a pixel size of 3 by 3 m, were then added together to get a development surface. Finally, we wanted to characterize each 30 by 30 m pixel in the basin by the proportion that it was developed.

One hundred 3 by 3 m pixels fit into one 30 by 30 meter pixel. We overlaid a grid (with a pixel size of 30 m) on the entire basin, and for each 30 meter pixel, we counted the number of 3 by 3 m pixels that were developed. Values ranged from 0 to 100. A value of zero implied that there is no development within the pixel, and a value of 100 implied that the entire pixel was developed. This product was our final modeled development.

Once the sampling frame was completed, we randomly selected sites along the development gradient. We created 6 development classes: extremely low = no development within 500 m, very low = no development within 300 m, low = < 15% developed within 300 m, moderate = > 15 to 30% developed within 300 m, high = > 30 to 45% developed within 300 m, very high = > 45 to 60 % developed within 300, and extremely high = > 60%.

Chapter 2: Birds

Introduction

Birds have long been a model system for studying fragmentation, in part because of conservation concerns, public interest, and ease of surveying. Known effects of fragmentation and urbanization on bird communities include declines in species richness (Estades and Temple 1999); nestedness, such that species-poor communities are subsets of the species in species-rich communities (Bolger et al. 1991, Wright et al. 1998, Fernández-Juricic 2000a); loss of particular species, such as habitat specialists, dietary specialists, larger-bodied species, and species at high trophic levels (Wiens 1989, Newton 1998, Austen et al. 2001); and increases in generalist and exotic species (Austen et al. 2001). Lower nesting success frequently results from higher nest predation (Wilcove 1985, Wilcove and Robinson 1990, Robinson et al. 1995, Burke and Nol 2000), from increased parasitism by brown-headed cowbirds (*Molothrus ater*; (Wilcove and Robinson 1990, Robinson et al. 1995), and potentially from resource limitation (Wilcove and Robinson 1990, Robinson 1998). Although changes at the population level can help explain patterns at the community level, few studies of birds have simultaneously addressed responses of bird populations and communities to development and disturbance (Marzluff et al. 2001).

Methods

We used four techniques to determine species composition, density, reproductive success, and behavioral patterns in passerine and other birds that are readily detected by sight and sound: point counts, nest monitoring, behavioral observations, and spot mapping. Point counts enable the estimation of species density and community composition of birds in proximity to count stations, but do not provide information on territories or reproduction (Ralph et al. 1993). Nest monitoring (Martin and Geupel 1993) confirms the breeding status of species and provide estimates of reproductive success and rates of nest predation and parasitism. Observations of foraging behavior were intended to determine the locations and substrates of foraging attempts. We ceased spot mapping after the 2003 season, as we felt our effort would be better spent on other protocols; eliminating spot mapping allowed us to achieve much greater sample sizes for point counts and nest monitoring.

Point Counts

We conducted point counts to characterize the species composition of the sample unit and its landscape context. We established five point count stations; they resided at the center point and at approximately 200 m north, east, south and west of the center point (the “satellite” point counts; actual locations depended on access). Counts were 10 minutes in duration, during which we recorded all birds seen or heard, noting the location in one of six distance categories (0-25 m, 25-50 m, 50-75 m, 75-100 m, > 100 m, and flyovers). We conducted counts three times in the breeding season (mid-May to mid-July), with visits separated by at least one week. We began counts at least 15 min after sunrise and completed them before 9:30 a.m.

Nest Monitoring

We selected focal species that were the primary target of nest searching and monitoring. We intended the focal-species approach to nest searching to ensure adequate sample sizes to calculate nest success for at least a few species. Patterns in focal species cannot necessarily be generalized to guilds or the entire bird community. The selection of focal species was guided by the following criteria: they 1) were associated with conifer forest; 2) were common in the Lake Tahoe basin; 3) were associated with the understory for breeding or foraging; 4) nested low enough (< 40 ft off the ground) that nests were a) likely to be affected by anthropogenic disturbance, and b) feasibly monitored without climbing trees; 5) had a moderate or better ease of their nests being located; 6) were potentially an indicator of forest condition, including vulnerability to human disturbance and cowbird parasitism; 7) were potentially an indicator of other species or species groups; and 8) were complementary with other focal species such that the suite of focal species represented a diversity of life history characteristics (e.g., nest type, nest location, body size, diet). We determined the above characteristics for each species known to occur in the Lake Tahoe basin (Schlesinger and Romsos 2000) from Ehrlich et al. (1988), Baicich and Harrison (1997), USDA (2000), and personal knowledge. In addition, we selected a few species to examine for changes in nest-site characteristics along the development gradient. In all, we selected 12 focal species (Table 2.1).

Table 2.1. Focal species selected for monitoring nest success and assessing nest-site selection along a gradient of urbanization in the Lake Tahoe basin, 2003 to 2005.

Common name	Scientific name	Years
Open nesters		
American Robin	*Turdus migratorius*	2003-2004
Dark-eyed Junco	*Junco hyemalis*	2003-2005
Dusky Flycatcher	*Empidonax oberholseri*	2003-2005
Steller’s Jay	*Cyanocitta stelleri*	2003-2005
Western Wood-pewee	*Contopus sordidulus*	2003-2005
Cavity nesters		
Hairy Woodpecker	*Picoides villosus*	2003-2005
Mountain Chickadee	*Poecile gambeli*	2003-2004
Northern Flicker	*Colaptes auratus*	2003-2005
Pygmy Nuthatch	*Sitta pygmaea*	2003-2005
Red-breasted Nuthatch	*Sitta canadensis*	2003-2005
White-breasted Nuthatch	*Sitta carolinensis*	2003-2005
White-headed Woodpecker	*Picoides albolarvatus*	2003-2005

We searched for and monitored nests throughout each sample unit up to 200 m away from the center point. There was no strict time limit on the amount of searching allowed in each sample unit (Friesen et al. 1999, Burke and Nol 2000); our main objective was to find and monitor as many nests as possible. Generally, we located nests by observing the behavior and movements of individual birds. We revisited nests every 3 to 4 days to record breeding phase (nest building, egg laying, incubating, nestlings, fledged) and reproductive effort (number of eggs and young). We examined nests above eye level and those in cavities using a dental mirror, a small mirror secured to a 5-m telescoping pole, or a video camera mounted to a 15-m telescoping pole. We monitored activity of nests into which we could not see to determine breeding phase and eventual success or failure only. We followed guidelines in the BBIRD protocol (Martin et al. 1997) and Martin and Geupel (1993) for finding and monitoring nests and avoiding disturbance of nesting birds.

We included in nest survival analyses only nests that were shown to be active, thus removing from further analysis all nests that never progressed beyond the construction phase. We determined activity status of nests whose contents could not be viewed by analyzing the behavior of adults; for example, if a bird was sitting on the nest or occupying a nest cavity, then we assumed that egg-laying, incubation, or brooding was occurring.

In 2005, we re-appropriated our effort to focus nest monitoring on 1) species that appeared to show a difference in nest success across the development gradient, and 2) species for which we needed greater sample sizes. We ceased monitoring nests of all three species of nuthatch and the Northern Flicker; for these species we simply confirmed that nests were active and then collected nest-site selection data upon nests' completion.

Behavioral Observations

We conducted behavioral observations during the course of searching for nests in 2003 and 2004 to determine whether foraging substrate use and foraging height differed along the urbanization gradient. Birds encountered were observed for 20 seconds. For the first 10 seconds no data were taken, to allow time for the bird to return to its activity before being encountered by the observer. During the remaining 10-second period, observers noted the following information: species, time, perch substrate, height, distance from bole, and activity, and if the bird made a foraging attempt during that time, the foraging maneuver, foraging substrate, species, decay or decadence class, height, and diameter at breast height were also recorded. In 2004, data collected consisted of species, time, substrate, substrate species, and height. Observers were allowed to continue observations for five additional 10-second intervals to increase the chances that a foraging attempt would be observed. Only one 10-second interval was used for any given observation.

Explanatory Variables

We took basic measurements of vegetation structure and human development at each satellite point count station to complement data from the center point generated by the plant community component of the study. We measured trees, snags and logs and counted pieces of trash within 17.6 m; measured overall tree and shrub canopy cover and the proportion of that cover that individual species comprised; estimated proportion of the area within 30 m of the point that was occupied by various types of development; and estimated the distance to water, riparian vegetation, and development of various types

(Table 2.2). We also calculated numerous GIS variables such as elevation, percent slope, Normalized Vegetation Difference Index (NDVI), distance to permanent water, percent development at multiple spatial scales, and percent of conifer forest, shrubs, and aspen/riparian at multiple spatial scales (Table 2.2). We transformed explanatory variables as necessary to reduce the influence of outliers and account for nonlinearities in relationships with dependent variables; sometimes this involved adding a quadratic term. We standardized all variables by subtracting the mean and dividing by the standard deviation.

Once a nest either fledged or failed, we recorded the following characteristics of each nest with confirmed breeding: nest height; substrate species, height, and diameter at breast height; nest orientation; distance from and orientation to roads, trails, and development; canopy cover at the nest; and percent slope. We established an 11.3-m radius vegetation plot (Martin et al. 1997), in which we measured all trees and snags and recorded proportions of different categories of ground cover. We also calculated several GIS variables as described in Table 2.2.

Data Analysis

Community Structure

We subset the point count data for analyses of richness, abundance, dominance, and species composition. We used detections up to 100 m only and excluded waterbirds and raptors, for whom point counts in forests are not reliable detection methods, and nonnative species, resulting in 67 species being retained. We will refer to this subset from now on as “landbirds.”

Because of the potential for increased noise in urban areas to reduce detectability of landbirds, and the importance of addressing detectability in biological surveys (Buckland et al. 2001), we intended to use program DISTANCE (Thomas et al. 2004) to adjust abundance values for detectability. However, our desire for site-specific density estimates was thwarted by insufficient sample sizes on a site-by-site basis (the analysis requires 60-80 samples for a reasonable detection function, far beyond the typical abundance of birds at a given sample site); further, using development or some other surrogate for noise as a covariate in multiple covariate distance sampling (Buckland et al. 2001) would have precluded our use of development as a predictor in model selection. An analysis including all species showed a decline in detectability in higher development classes, but this appeared to be driven by a handful of common species. Further, 7 of 13 individual species for which we could generate acceptable detection functions showed no differences in detectability by development class; thus, adjusting abundances of all species based on the global model would have likely overcorrected, perhaps for over half the species. Because of these results, we determined that using raw abundance values in all analyses was most defensible.

Table 2.2. Explanatory variables used in analyses of landbird community structure in the Lake Tahoe basin, 2003-2005.

Variable code	**Variable**	**Source**	**Transformations**
Development			
Dev30	Percent of area within 30 m occupied by development	Field estimate	
Dev150,Dev150^2 Dev300,Dev300^2 Dev500,Dev500^2 Dev1000,Dev1000^2	Percent of area within 150, 300, 500, or 1000 m occupied by development	GIS development model	sq
Landscape-level vegetation			
Conif150,300,500,1000 AsRi150,300,500,1000 Shrubs150,300,500,1000	Percent of area within 150, 300, 500, or 1000 m occupied by conifer forest, aspen forest/riparian, or shrubs	Dobrowski et al. (2005) vegetation layer for the basin, crosswalked to CWHR type	
Habdiv150,300,500,1000	Number of habitat types within 150, 300, 500, or 1000 m	Dobrowski et al. (2005) vegetation layer for the basin, crosswalked to CWHR type	
Local vegetation structure			
NDVI,NDVIpos^2,NDVI^2	Normalized Difference Vegetation Index (essentially a measure of productivity) averaged within 100 m	GIS layer derived from 2001 Landsat TM image	Scaled to make all values positive, then sq
Shrubs30,Shrb30Rt	Percent cover of shrubs within 30 m	Field estimate	sqrt
CanCov,CanCov^2	Canopy cover	Average of 16 field measurements	
TreesRt	Tree density; number of trees within 17.6 m	Field measurement	sqrt
SngVolLg	Snag volume, based on DBH and height; cylindrical shape assumed	Field measurement	ln(x+1)
CWD_log	Coarse woody debris	Field measurement	ln(x+1)
Herbs	Percent cover of herbs and grass within 30 m	Field measurement	
Abiotic factors			
Elev	Elevation, average over area within ~50 m	Digital elevation model	

Variable code	Variable	Source	Transformations
$Slp100, Slp100^2$	Percent slope, average over area within 100 m	Digital elevation model	sq
$DistWtr, DistWtr^2$	Distance to permanent water	GIS	sq
Human use			
People	Number of people encountered per hour	Field surveys	
Dogs	Number of dogs encountered per hour	Field surveys	
Vehic_lg	Number of vehicles encountered per hour	Field surveys	ln(x+1)
Geographical location			
UTM N, UTM N^2	Northing	GPS measurement	sq
UTM E	Easting	GPS measurement	

We calculated summary variables of the bird community using two subsets of the data depending on the explanatory variables of interest. For analyses examining the effects of human use, we used only point count results from the center point (n = 75), as the human use data were collected within 100 m of the center. For analyses of total species richness and abundance, we treated each count station (n = 375) as a sample; we used Durbin-Watson tests to ensure that stations were independent, and additionally analyzed only center-point-count data to examine the importance of human use. We calculated species richness at each count station as the total number of landbird species detected in three visits. We calculated abundance of all species, species groups, and individual species as the average number of individuals detected in three visits to each count station. (At one site [L14], data were unavailable for a single visit to one of the count stations; thus, for that station, we calculated the average over two visits.) We calculated dominance using the Berger-Parker index (Magurran 1988), which is simply the abundance of the most abundant species divided by the total abundance. We transformed dependent variables as necessary to achieve normality, using log, square, and square-root transformations (Sokal and Rohlf 1995). Normality could not be achieved in all cases.

To examine whether species composition varied among categories of urbanization, we used the multi-response permutation procedure (MRPP), which is a nonparametric method that tests for differences among groups using similarity metrics based on presence-absence data (McCune and Grace 2002). We used Sørenson's distance as the similarity measure and ran the MRPP with a series of 1000 permutations of group associations. For each group, we applied a natural weighting factor ($n/\Sigma\,[n]$) to the samples. Significance values were based on permutation distributions (McCune and Mefford 1999). Presence and absence were based on the entire five-station array at each site. We tested for differences in composition among three categories based on development level within 300 m: 0-1% development (10 sites), 1-30% development (31 sites), and >30% development (34 sites). The test statistic, T, is a measure of the difference in composition among sites with 0-1% development, 1-30% development, and >30% development. The ΔT value represents the change in T with each species removed from the analysis; species were replaced in all other analyses. Positive values of ΔT represent species whose presence makes species composition more different among development categories, while negative values represent species whose presence makes species composition more similar. A measure of within-group similarity, A, is also presented, with values near zero demonstrating within-group heterogeneity similar to that expected by chance. Subsequent to the MRPP, we removed one species at a time with replacement to determine which species were driving any observed changes in composition. Species that caused a large change in the test statistic were ones that had a large influence on differences in composition.

We constructed a rank-abundance plot to examine changes in the relative importance of species in community structure in three levels of development. We used all 375 count stations independently and used the same three development categories: 0-1% development (46 count stations), 1-30% development (156 count stations), and >30% development (173 count stations).

We used model selection to determine important categories of factors affecting various landbird community metrics. We used a second-order variation of Akaike's Information Criterion (AIC) that adjusts for small sample sizes (AIC_c) to compare candidate models. Model selection using AIC is an information-theoretic method that allows comparison of multiple competing models that represent scientific hypotheses. It involves an explicit recognition of model selection uncertainty and does not rely on statistical significance testing, which can be highly arbitrary (Burnham and Anderson 2002). Candidate models are enumerated in advance and their AIC_c values compared. Akaike weights, which represent the strength of evidence of support for each model and total to 1 for all models, are calculated. The importance of individual variables (or, in our case, factor groups; below) is determined by adding Akaike weights for all models in which each variable (or group) appears.

We considered combinations of factor groups (collections of like variables) in different models rather than individual variables, because using the number of potentially important individual variables would have far exceeded the recommended number of models for our sample sizes (Anderson et al. 2001). A similar approach was used by Van Buskirk (2005). The factor groups we included were ones shown to affect landbirds in other studies: geographical location, abiotic factors, landscape-level vegetation, local vegetation structure, development, and human use (Table 2.2). We determined the best model in two steps. First, to avoid overfitting models, we determined the best submodel for each factor group by fitting a global submodel (e.g., all local vegetation structure variables), and then removing variables one by one with replacement and retaining in the final submodel only those variables whose inclusion improved (lowered) the AIC_c for that submodel. Thus, a subset of the variables in each factor group was promoted for consideration in overall models. We did not do this for geographic location (UTMs); rather, we always included both northing and easting coordinates in models with the geography factor group. In the case of development and landscape-level vegetation, for which multiple spatial scales could be suitable, we used model selection to determine which of four or five possible spatial scales was most explanatory: 30 m (not available when only the center point count was considered, as those points were selected to be in forest and nearly all values were zero), 150 m, 300 m, 500 m, and 1000 m. For vegetation scales, we first determined the most appropriate scale(s), and subsequently determined the best submodel.

We considered all combinations of five (when human use was excluded and 375 count stations were included) or six (when human use was included and only the 75 center count stations were included) categories of variables in our overall models (Table 2.2), yielding 31 or 63 candidate models to be compared against one another. For the AIC_c-best overall model, we determined which individual variables were most important by examining the change in AIC_c when each variable was removed. The change in AIC_c with a variable's removal suggested the degree to which the variable improved the overall model or made it worse.

In this report, we examined important factors affecting richness of all species and abundance of all species, ground nesters, cavity nesters, ground-foraging omnivores, and invertivores. We chose these functional groups to reflect a variety of ecological characteristics that might predispose species to be sensitive to human use and changes in habitat brought about by urbanization. Some of these groups, like ground nesters, we expected to decrease with urbanization. Cavity nesters, too, might decrease with a decrease in the amount of snags resulting from development or human activities. Many ground-foragers should likewise be sensitive to human disturbance and ground-level habitat changes, but those that are omnivorous should thrive, as they likely benefit from a wide variety of human-provided food often located on the ground. Invertivores could decrease if their prey base is rendered less abundant by changes in vegetation in urban areas.

Productivity

We used the logistic-exposure method to calculate nest success (Shaffer 2004). In this method, rather than the success or failure of individual nests being of interest, intervals of observation are samples, with the dependent variable in the analysis being survival or failure of the nest during the observation interval. The method is essentially a hybrid of Mayfield-style (1975; Johnson 1979) exposure methods, which recognize that nests found at later stages are more likely to be successful than those found at earlier stages, and logistic regression methods, which allow modeling of covariates thought to affect nest survival. Survival or failure is modeled as a function of the length of the observation interval, known as the "exposure," and any covariates the investigator deems potentially important to nest success. A model selection approach is employed, with candidate models compared against one another using AIC_c. Model-averaged parameters (Burnham and Anderson 2002) are used to generate a daily survival rate (DSR), which can be raised to the power of the length of the nesting period to arrive at a probability of nest success. Thus, nest success in this method is not the proportion of nests successful in the sample, but is the probability that an individual nest in the population will succeed.

For each species or species group of interest, we first modeled the effects of date (number of days since May 15) and year as a categorical predictor to examine time-specific nest success (Grant et al. 2005; Purcell 2006). We also modeled survival as a quadratic function of date, to allow for the possibility of increased survival midseason.

The best time-specific model was used as the starting model in all future analyses, rather than the "constant-survival" model that is otherwise used as a null model. This approach allowed us to account for any potential bias in locating with differing frequencies nests with varying probabilities of success in different years or times of the season.

We modeled DSR of all open nesters versus all cavity nesters, guilds of open and cavity nesters, and all individual species for which we had a reasonable number of nests (Table 2.1). We used development at various scales, nest substrate, and nest height (in addition to any time-specific covariates retained from the time-specific models) as covariates, depending on the species or species group. We used one of three development scales in each model: 50 m, 100 m, and 300 m, to represent local and neighborhood scales of development. Only one development scale was present in each model. We examined nest substrate if the species or species group used two or more substrates with sufficient frequency. We examined nest height if the species or species group used a variety of nest heights. We constructed candidate models consisting of all possible combinations of categorical main effects and covariates.

Habitat Use: Nest-site Selection

We investigated whether birds might select nest-site habitat characteristics differently according to development and human use for species groups and individual species. We used a model selection approach similar to that used for richness and abundance (above), comparing models by AIC_c. We examined all possible combinations of 50-m development, 100-m development, 300-m development, and number of people detected per hour (log-transformed). We included only nests within 150 m of the center point, a reasonable approximation of the area within which the human-use data, collected at the center, could be expected to apply. We also examined nest substrate in two categories of development (≤ 30% and > 30%) using chi-square tests for goodness of fit. Analyses of use vs. availability and comparisons with surrounding vegetation are ongoing.

We also investigated whether species and species groups used different substrate types in different categories of development. We examined only species and species groups that showed some variation in use of general substrate types, which limited our analysis to cavity nesters and the Steller's Jay. We built categories of development based on percent development within 100 m of each nest; a 100-m radius defined an area over which birds might search for nest sites after establishing a territory. Boundaries of development categories differed according to the distribution of nests along the development gradient (Mountain Chickadee, White-breasted Nuthatch: 10% cutoff; primary cavity excavators, weak cavity excavators and secondary cavity nesters, Pygmy Nuthatch, White-headed Woodpecker: 15% cutoff; Northern Flicker: 20% cutoff; Steller's Jay: 30% cutoff). We used general substrate types such as "live" (trees, shrubs) and "dead" (snags, logs, stumps) because of the need for larger sample sizes in each cell of contingency tables; we omitted substrates used infrequently, such as human structures, from analysis when necessary and simply reported numbers of nests with those substrates. We used a G-test of independence to test for statistically significant differences in substrate use by development category, as neither factor was fixed by the investigators (Sokal and Rohlf 1995).

Habitat Use: Foraging

For analysis of foraging heights, we used only the first observation period in which the bird was foraging, as repeated observations on single birds are not necessarily independent (Raphael 1990). We calculated the proportion of observations of foraging birds in different height classes and substrate types and examined these in relation to categories of development. Percent development was based on the center point, not the location of the bird, which we did not record. We examined foraging heights (in two categories, 0-3 m and >3 m) in two categories of development (≤ 30% and > 30%) using chi-square tests for goodness of fit.

Results

Sampling Completed

From May-July of 2003 and 2004, we surveyed the point count array at 75 sample sites that spanned the development gradient and were balanced by basin orientation. From May-August of 2003, 2004, and 2005, we located and monitored nests in those sites and an additional 22 sites, for a total of 97 sites. We took habitat measurements in July-September of 2003, 2004, and 2005 at 570 nest sites and 300 satellite point count stations.

Community Structure

We detected 21,726 individual birds of 67 native landbird species in total, excluding waterbirds and raptors. Species richness ranged from 5 to 28 at the 375 count stations ($\bar{x}$ = 16.0, s.e. = 0.20). Abundance ranged from 5.3 to 59.0 ($\bar{x}$ = 19.3, s.e. = 0.29).

MRPP analysis showed significant differences in species composition among low-, moderate-, and high-development sites ($T = -13.593$, $P < 0.0001$). Low-development sites were significantly different from moderate-development sites ($T = -3.635$, $P = 0.0038$) and high-development sites ($T = -14.261$, $P < 0.0001$); moderate-development sites were significantly different from high-development sites ($T = -10.972$, $P < 0.0001$). Species making the largest contribution to the differences in composition among development categories ($\Delta T > 0$) were Brewer's Blackbird, Dusky Flycatcher, White-breasted Nuthatch, Hermit Thrush, and Cassin's Vireo (Table 2.3), which were species whose frequency of occurrence varied greatly among development categories. Species that were either present nearly at all sites (e.g., Mountain Chickadee, Steller's Jay) or that were present at very few sites (e.g., Rufous Hummingbird, Lesser Goldfinch) had no influence on the compositional difference among development categories ($\Delta T \approx 0$) (Table 2.3). Species with a similar frequency of occurrence in the three development categories, but with lower overall frequency of occurrence (e.g., MacGillivray's Warbler, Golden-crowned Kinglet) tended to make the development categories more similar in composition ($\Delta T < 0$) (Table 2.3).

Table 2.3. Results of Multi-Response Permutation Procedures analysis on composition of 67 landbird species at 75 sites in the Lake Tahoe basin, 2003-2004.

Species removed from analysis	T	ΔT	A
All 67 species included	-13.594	-	0.0737
Brewer's Blackbird	-11.930	1.664	0.0624
Dusky Flycatcher	-12.205	1.389	0.0645
White-breasted Nuthatch	-13.033	0.561	0.0714
Hermit Thrush	-13.113	0.481	0.0703
Cassin's Vireo	-13.151	0.442	0.0711
Pileated Woodpecker	-13.218	0.375	0.0720
Green-tailed Towhee	-13.220	0.373	0.0722
Band-tailed Pigeon	-13.268	0.326	0.0729
Hairy Woodpecker	-13.312	0.282	0.0733
Barn Swallow	-13.364	0.229	0.0731
Tree Swallow	-13.435	0.159	0.0736
Chipping Sparrow	-13.445	0.149	0.0739
Hermit Warbler	-13.477	0.117	0.0729
Townsend's Solitaire	-13.483	0.110	0.0725
Olive-sided Flycatcher	-13.512	0.081	0.0729
Wilson's Warbler	-13.525	0.069	0.0734
Williamson's Sapsucker	-13.527	0.066	0.0738
Clark's Nutcracker	-13.544	0.050	0.0749
Brown Creeper	-13.547	0.046	0.0740
Cassin's Hummingbird	-13.572	0.022	0.0738
Black-billed Magpie	-13.579	0.014	0.0738
Savannah Sparrow	-13.579	0.014	0.0738
Common Nighthawk	-13.580	0.013	0.0740
Mountain Quail	-13.581	0.013	0.0741
American Robin	-13.581	0.013	0.0736
Brown-headed Cowbird	-13.586	0.007	0.0736
Purple Finch	-13.590	0.003	0.0740
Lincoln's Sparrow	-13.592	0.002	0.0738
Mourning Dove	-13.592	0.002	0.0741
Mountain Chickadee	-13.593	0.000	0.0736
Steller's Jay	-13.593	0.000	0.0736
Rufous Hummingbird	-13.595	-0.001	0.0738
Lesser Goldfinch	-13.595	-0.002	0.0741
Blue Grouse	-13.598	-0.004	0.0738
Bushtit	-13.600	-0.006	0.0739
House Finch	-13.601	-0.007	0.0739
Yellow-rumped Warbler	-13.601	-0.008	0.0740
American Crow	-13.603	-0.010	0.0739
Black-backed Woodpecker	-13.604	-0.010	0.0740
Yellow-headed Blackbird	-13.604	-0.011	0.0740
Cliff Swallow	-13.604	-0.011	0.0739
Yellow Warbler	-13.612	-0.019	0.0740
Common Raven	-13.613	-0.019	0.0751
Dark-eyed Junco	-13.613	-0.019	0.0739
Red-winged Blackbird	-13.615	-0.022	0.0741
Northern Flicker	-13.616	-0.022	0.0742

Species removed from analysis	T	ΔT	A
Pygmy Nuthatch	-13.636	-0.042	0.0738
Pine Grosbeak	-13.636	-0.043	0.0743
Western Tanager	-13.639	-0.046	0.0745
Black-headed Grosbeak	-13.646	-0.053	0.0746
House Wren	-13.649	-0.055	0.0747
White-headed Woodpecker	-13.661	-0.067	0.0750
Red Crossbill	-13.670	-0.076	0.0756
Evening Grosbeak	-13.682	-0.089	0.0754
Downy Woodpecker	-13.697	-0.103	0.0754
Warbling Vireo	-13.717	-0.123	0.0742
Nashville Warbler	-13.737	-0.143	0.0734
Red-breasted Nuthatch	-13.738	-0.145	0.0757
Red-breasted Sapsucker	-13.738	-0.145	0.0757
Fox Sparrow	-13.742	-0.149	0.0750
Western Wood-pewee	-13.745	-0.152	0.0756
Song Sparrow	-13.762	-0.168	0.0752
Pine Siskin	-13.824	-0.230	0.0759
Cassin’s Finch	-13.830	-0.237	0.0766
Spotted Towhee	-13.860	-0.266	0.0759
Golden-crowned Kinglet	-13.914	-0.320	0.0756
MacGillivray’s Warbler	-13.924	-0.331	0.0760

Model selection highlighted important development, landscape-level vegetation, local habitat, abiotic, geographic, and human use factors affecting bird species groups. Landbird species richness was most influenced by a combination of development, local habitat, abiotic, and geographic factors, with northing ($\Delta AIC_c = 15.20$), slope ($\Delta AIC_c = 12.79$), 1000-m development ($\Delta AIC_c = 9.13$), and distance to water ($\Delta AIC_c = 9.00$) being most important (Table 2.4, Fig. 2.2). A subsequent analysis on the 75 center point counts only showed species richness to be most influenced by human activity (Fig. 2.2b). Abundance of all birds was most influenced by landscape-level vegetation, abiotic, and geographic factors, with elevation ($\Delta AIC_c = 18.61$) and 1000-m shrubs ($\Delta AIC_c = 12.32$) being most important (Table 2.5, Fig. 2.3). A subsequent analysis on the 75 point counts only showed abundance to be most influenced by similar factors (Fig. 2.2b). Dominance was influenced most by development and landscape-level vegetation (Fig. 2.2b).

Abundance of bird species guilds were variously associated with development (Appendix 2.1), as were bird families (Appendix 2.2). Factors influencing abundance of species groups varied widely. Abundance of ground nesters was influenced most by landscape, abiotic, and geographic factors (Table 2.6, Fig. 2.3). The most important variables in the best model, although considerable model selection uncertainty existed, were 300-m conifer ($\Delta AIC_c = 4.39$) and easting ($\Delta AIC_c = 2.10$). Abundance of cavity nesters was influenced most by human use, local habitat, abiotic factors, landscape factors, and geography, with considerable model selection uncertainty (Table 2.7, Fig. 2.4). The most important variables in the best model were snag volume ($\Delta AIC_c = 7.92$) and dogs ($\Delta AIC_c = 6.84$). The relationship between cavity nesters and snag volume suggest that snag volumes of > 10 m3/ha were required to support the full potential of cavity nester abundance (Fig 2.5).

Abundance of ground-foraging omnivores was most influenced by human use, landscape-level vegetation, and local habitat (Table 2.8, Fig. 2.6). The most important variables in the best model were dogs ($\Delta AIC_c = 21.20$) and 1000-m conifer ($\Delta AIC_c = 10.92$). Abundance of invertivores was most influenced by abiotic factors and local habitat, with percent slope ($\Delta AIC_c = 4.76$), tree density ($\Delta AIC_c = 4.61$), and canopy cover ($\Delta AIC_c = 3.78$) being the most important variables in the best model (Table 2.9, Fig. 2.7). The relationship between invertivore abundance and tree density showed a steady decline in the maximum abundance as tree density increased (Fig. 2.8). Tree diameter typically declines as tree density increases, thus this suggests that invertivore abundance also with declines with tree diameter.

Model selection for landbirds at point count stations along a development gradient are presented in Tables 2.4 to 2.9 (variable definitions are in Table 2.2). Comparison of submodels of development, local habitat, landscape-level vegetation, abiotic factors, and geography variables in full and reduced form are presented. The direction of the effect of each variable in the best submodel is given in parentheses. In addition, the best overall models, generated from all possible combinations of reduced submodels, with the addition of the full geography submodel. Models with AIC_c weights of 0.05 or greater are reported. The importance of each factor group is evaluated as determined by Akaike weights summed across all models containing that group.

Table 2.4. Landbird species richness (n = 375 count stations); a) submodel comparison, b) best overall models, c) importance of factor groups.

a)

Model	Variables	AIC_c	Weight
Full submodels of factor groups			
Development	Dev30,150,300,500, 1000	1978.04	1.000
Landscape	AsRi150,300,500,1000, Conif150,300,500,1000 Shrub150,300,500,1000, Habs150,300,500,1000	2033.24	0.000
Local	$NDVIpos^2$, Shrb30Rt, CanCov, TreesRt, SngVolLg , Herbs	2004.50	0.000
Abiotic	Elev, Slp100, $Slp100^2$, DistWtr	2056.04	0.000
Geography	UTM N, UTM N^2, UTM E	2060.24	0.000
Reduced submodels			
Development	Dev30 (-), Dev150 (-), Dev1000 (-)	1975.19	
Landscape	AsRi300 (+), Conif300 (+), Shrub300 (-)	2018.03	
Local	$NDVIpos^2$ (+), Shrb30Rt (+), CanCov (-), TreesRt (+), SngVolLg (+), Herbs (+)	2004.50	
Abiotic	Slp100 (-), $Slp100^2$ (+), DistWtr (-)	2054.10	

b)

Factor groups included in best models	AIC_c	Weight	Adj. R^2
Development, local, abiotic, geography	1933.55	0.697	0.366
Development, local, landscape, abiotic, geography	1935.48	0.266	0.368

c)

Factor group	Sum of model weights
Development	1.000
Landscape	0.296
Local	0.965
Abiotic	1.000
Geography	0.998

Table 2.5. Landbird abundance (n = 375 count stations); a) submodel comparison, b) best overall models, c) importance of factor groups.

a)

Model	Variables	AIC$_c$	Weight
Full submodels of factor groups			
Development	Dev30,150, 300,500,500^2,1000,1000^2	718.32	0.000
Landscape	AsRi150,300,500,1000, Conif150,300,500,1000 Shrub150,300,500,1000, Habs150,300,500,1000	718.33	0.000
Local	NDVIpos^2, Shrub30, CanCov, TreesRt, SngVolLg , Herbs	720.91	0.000
Abiotic	Elev, Slp100, DistWtr	684.76	1.000
Geography	UTM N, UTM E	704.85	0.000
Reduced submodels			
Development	Dev300 (+), Dev1000 (+), Dev1000^2 (-)	710.06	
Landscape	Conif1000 (-), Shrb1000 (-), Habs1000 (-)	697.05	
Local	NDVIpos^2 (-), Shrub30 (-), CanCov (-), TreesRt (-), Herbs (+)	718.83	
Abiotic	Elev (-), DistWtr (+)	683.13	

b)

Factor groups included in best models	AIC$_c$	Weight	Adj. R^2
Landscape, abiotic, geography	656.45	0.782	0.178
Landscape, local, abiotic, geography	659.82	0.145	0.193

c)

Factor group	Sum of model weights
Development	0.06
Landscape	1.00
Local	0.16
Abiotic	1.00
Geography	0.99

Table 2.6. Ground-nester abundance (n = 75 count stations); a) submodel comparison, b) best overall models, c) importance of factor groups.

a)

Model	Variables	AIC$_c$	Weight
Full submodels of factor groups			
Development	Dev150,300,500,1000	98.04	0.007
Landscape	AsRi150,300,500,1000, Conif150,300,500,1000 Shrub150,300,500,1000, Habs150,300,500,1000	107.81	0.000
Local	NDVI^2, Shrubs30, CanCov, TreesRt, SngVolLg, CWD_log, Herbs	99.07	0.004
Abiotic	Elev, Slp100, DistWtr, DistWtr^2	88.50	0.857
Geography	UTM N, UTM E	110.95	0.000
Human use	People, Dogs, Vehic_lg	92.26	0.131
Reduced submodels			
Development	Dev150 (-), Dev1000 (-)	93.56	
Landscape	AsRi300 (+), Conif300 (+)	84.88	
Local	NDVI^2 (+), TreesRt (-)	93.61	
Abiotic	Elev (+), Slp100 (+), DistWtr (+), DistWtr^2 (-)	88.50	
Human use	People (-), Dogs (+), Vehic_lg (-)	92.26	

b)

Factor groups included in best models	AIC$_c$	Weight	Adj. R^2
Landscape, abiotic, geography	78.42	0.196	0.462
Landscape, local, abiotic, geography	79.25	0.129	0.480
Landscape, abiotic	79.70	0.103	0.431

c)

Factor group	Sum of model weights
Development	0.28
Landscape	0.75
Local	0.33
Abiotic	0.85
Geography	0.57
Human use	0.34

Table 2.7. Cavity-nester abundance (n = 75 count stations); a) submodel comparison, b) best overall models, c) importance of factor groups.

a)

Model	Variables	AIC$_c$	Weight
Full submodels of factor groups			
Development	Dev150,300,500,1000	355.54	0.007
Landscape	AsRi150,300,500,1000, Conif150,300,500,1000 Shrub150,300,500,1000, Habs150,300,500,1000	368.48	0.000
Local	NDVI^2, Shrubs30, CanCov, TreesRt, SngVolLg, CWD_log	355.52	0.007
Abiotic	Elev, Slp100, DistWtr	353.40	0.020
Geography	UTM N, UTM E	345.97	0.822
Human use	People, Dogs, Vehic_lg	349.45	0.144
Reduced submodels			
Development	Dev150 (-)	350.00	
Landscape	Conif150 (+), Shrub150 (+)	346.02	
Local	SngVolLg (+), CWD_log (-)	348.73	
Abiotic	DistWtr (+)	350.21	
Human use	Dogs (+)	348.54	

b)

Factor groups included in best models	AIC$_c$	Weight	Adj. R^2
Local, abiotic, use	341.92	0.080	0.071
Landscape, local, geography, use	342.34	0.065	0.173
Landscape, geography	342.55	0.058	0.153

c)

Factor group	Sum of model weights
Development	0.294
Landscape	0.553
Local	0.647
Abiotic	0.447
Geography	0.748
Human use	0.586

Table 2.8. Ground-foraging omnivore abundance (n = 75 count stations); a) submodel comparison, b) best overall models, c) importance of factor groups.

a)

Model	Variables	AIC$_c$	Weight
Full submodels of factor groups			
Development	Dev150,150^2,300,300^2,500,500^2,1000,1000^2	115.93	0.622
Landscape	AsRi150,300,500,1000, Conif150,300,500,1000 Shrub150,300,300^2,500,1000, Habs150,300,500,1000	153.09	0.000
Local	NDVI^2, Shrubs30, CanCov, TreesRt, Herbs	129.35	0.001
Abiotic	Elev, Slp100, Slp100^2, DistWtr	119.52	0.103
Geography	UTM N, UTM E	156.31	0.000
Human use	People, Dogs, Vehic_lg	117.57	0.274
Reduced submodels			
Development	Dev150 (+),Dev150^2 (-), Dev1000 (+),Dev1000^2 (-)	109.63	
Landscape	Con1000 (-)	125.82	
Local	NDVI^2 (-), Herbs (+)	122.83	
Abiotic	Elev (-), Slp100 (-), Slp100^2 (+)	117.16	
Human use	Dogs (+), Vehic_lg (+)	116.40	

b)

Factor groups included in best models	AIC$_c$	Weight	Adj. R^2
Landscape, local, use	95.05	0.306	0.504
Landscape, local, geography, use	96.02	0.188	0.498
Development, landscape, local, use	96.68	0.135	0.575
Development, landscape, use	97.51	0.089	0.574
Landscape, use	97.70	0.081	0.489

c)

Factor group	Sum of model weights
Development	0.285
Landscape	0.994
Local	0.710
Abiotic	0.143
Geography	0.280
Human use	1.000

Table 2.9. Invertivore abundance (n = 75 count stations); a) submodel comparison, b) best overall models, c) importance of factor groups.

a)

Model	Variables	AIC$_c$	Weight
Full submodels of factor groups			
Development	Dev150,300,500,1000	398.83	0.067
Landscape	AsRi150,300,500,1000, Conif150,300,500,1000 Shrub150,300,500,1000, Habs150,300,500,1000	422.02	0.000
Local	NDVI^2, Shrubs30, CanCov, CanCov^2, TreesRt, SngVolLg, Herbs, CWD_log	400.96	0.006
Abiotic	Elev, Slp100, Slp100^2, DistWtr	393.71	0.865
Geography	UTM N, UTM E	400.08	0.036
Human use	People, Dogs, Vehic_lg	400.75	0.026
Reduced submodels			
Development	Dev150 (-)	393.92	
Landscape	Conif500 (+), AsRi500 (+)	394.09	
Local	CanCov (+), CanCov^2 (-), SngVolLg (+), TreesRt (-)	394.46	
Abiotic	DistWtr (+), Slp100 (+), Slp100^2 (-)	391.42	
Human use	Vehic_lg (-)	398.65	

b)

Factor groups included in best models	AIC$_c$	Weight	Adj. R^2
Local, abiotic, geography	382.46	0.196	0.359
Local, abiotic	382.80	0.165	0.328
Local, abiotic, use	383.54	0.114	0.335
Development, local, abiotic	384.19	0.082	0.329
Local, abiotic, geography, use	384.77	0.062	0.353
Development, local, abiotic, geography	384.93	0.057	0.352

c)

Factor group	Sum of model weights
Development	0.293
Landscape	0.201
Local	0.886
Abiotic	0.982
Geography	0.444
Human use	0.311

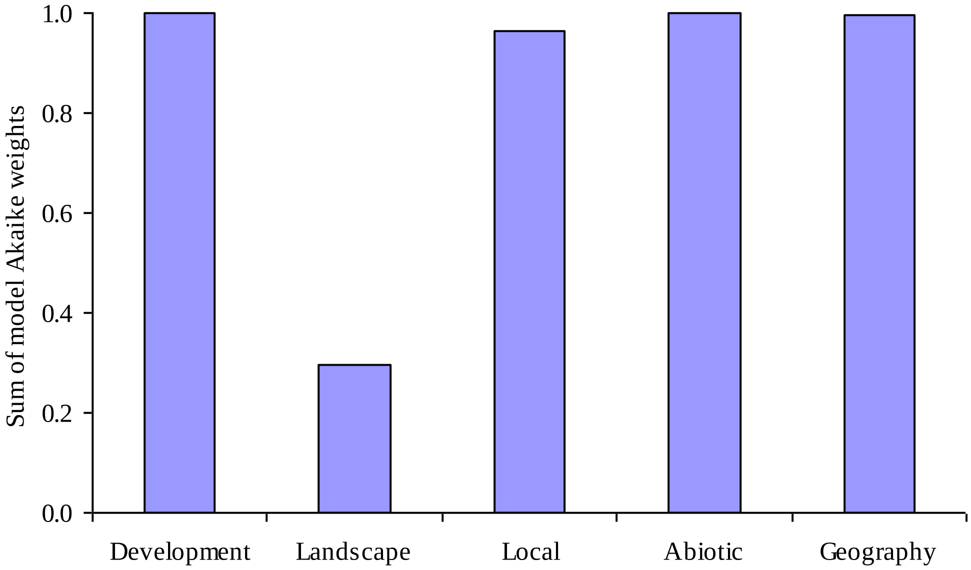


Figure 2.1. Association of five factor groups with landbird species richness from 375 count stations in the Lake Tahoe basin, 2003-2004. Importance of each factor group is measured by summing the Akaike weights of models containing that factor group. See Table 2.2 for specific variables comprising each factor group.

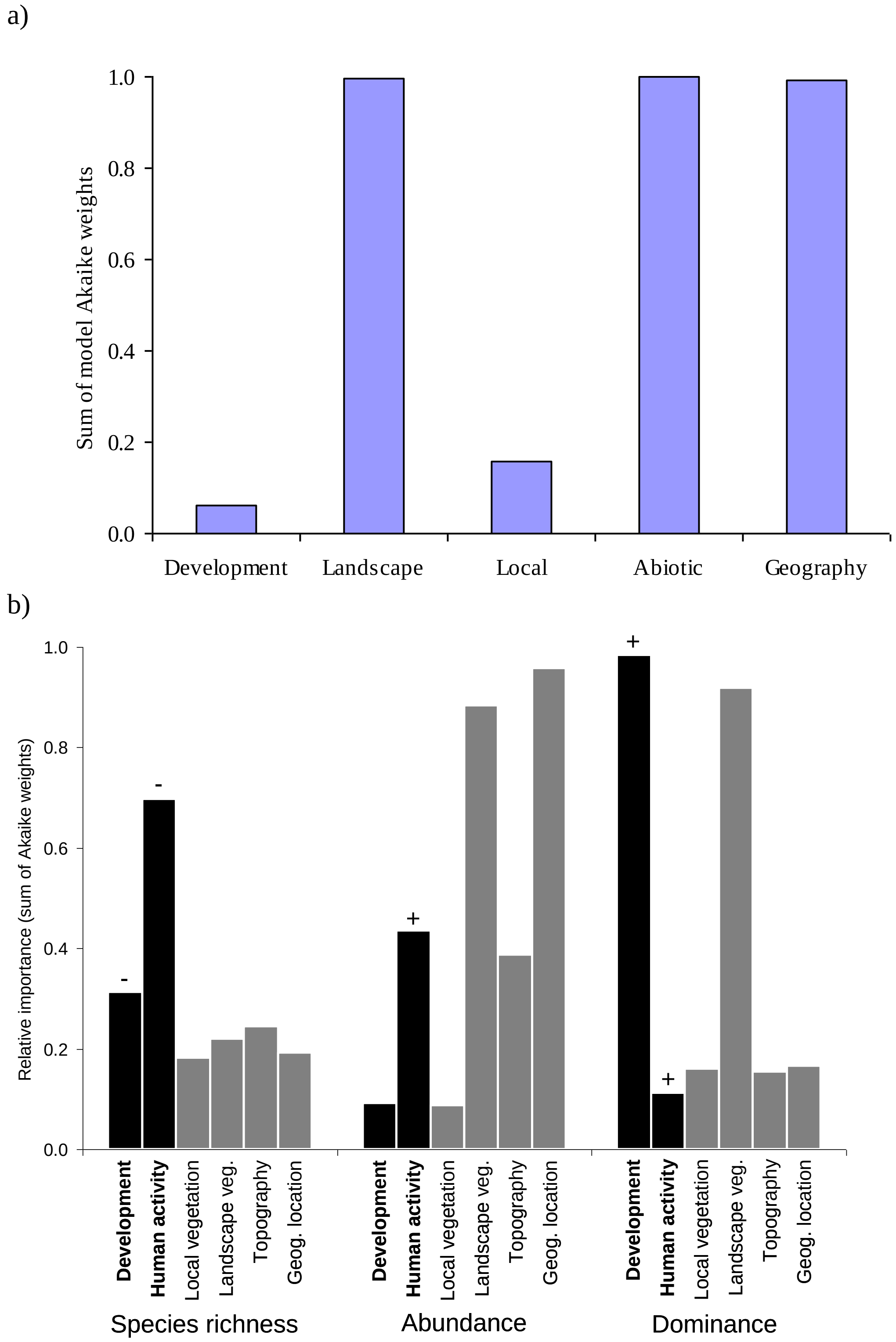


Figure 2.2. Association of five factor groups with landbird richness, abundance, and dominance. a) Abundance from 375 count stations in the Lake Tahoe basin, 2003-2004, and b) comparison of species richness, abundance and dominance from the center point count station. Importance of each factor group is measured by summing the Akaike weights of models containing that factor group. See Table 2.2 for specific variables comprising each factor group.

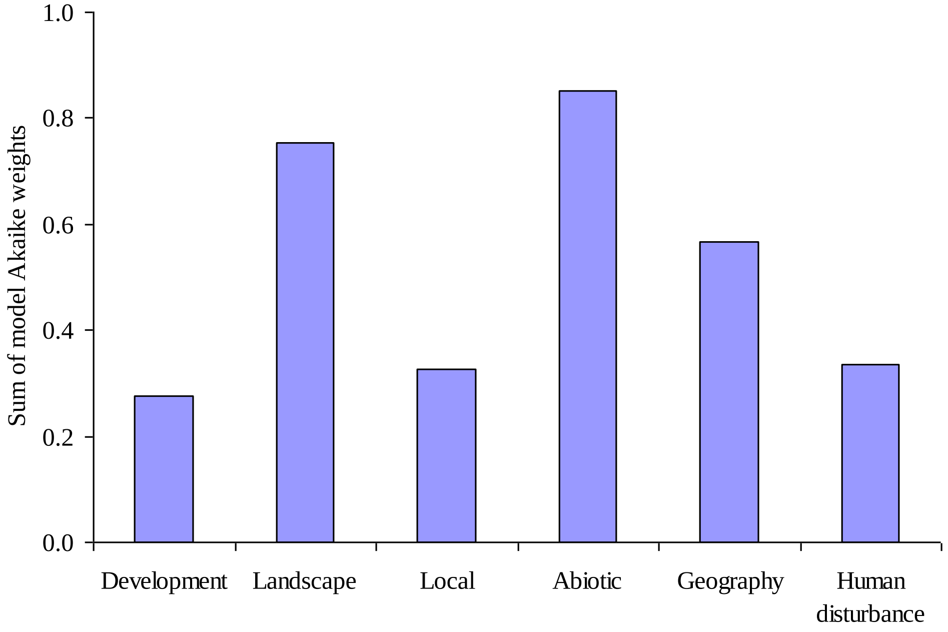


Figure 2.3. Association of six factor groups with abundance of ground-nesting landbirds from 75 count stations in the Lake Tahoe basin, 2003-2004. Importance of each factor group is measured by summing the Akaike weights of models containing that factor group. See Table 2.2 for specific variables comprising each factor group.

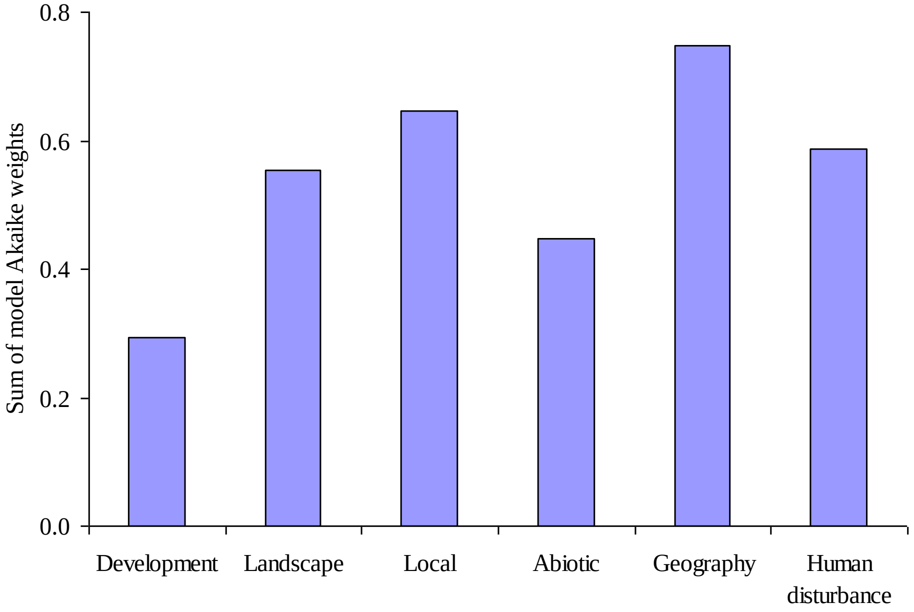


Figure 2.4. Association of six factor groups with abundance of cavity-nesting landbirds from 75 count stations in the Lake Tahoe basin, 2003-2004. Importance of each factor group is measured by summing the Akaike weights of models containing that factor group. See Table 2.2 for specific variables comprising each factor group.

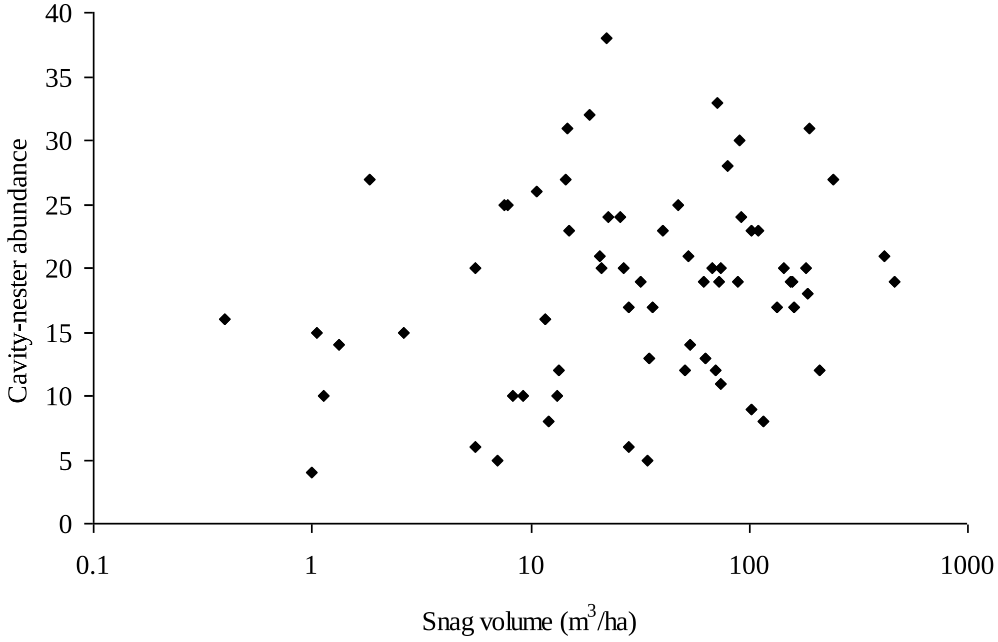


Figure 2.5. Abundance of cavity-nesting birds as a function of snag volume (plotted on a log scale) at 75 sites along a gradient of urban development in the Lake Tahoe basin, 2003-2004.

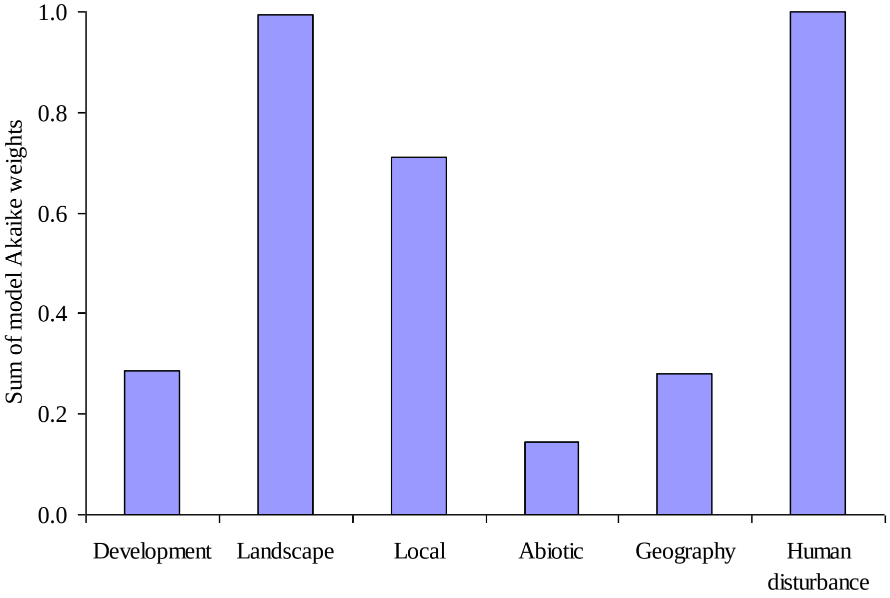


Figure 2.6. Association of six factor groups with abundance of ground-foraging omnivorous landbirds from 75 count stations in the Lake Tahoe basin, 2003-2004. Importance of each factor group is measured by summing the Akaike weights of models containing that factor group. See Table 2.2 for specific variables comprising each factor group.

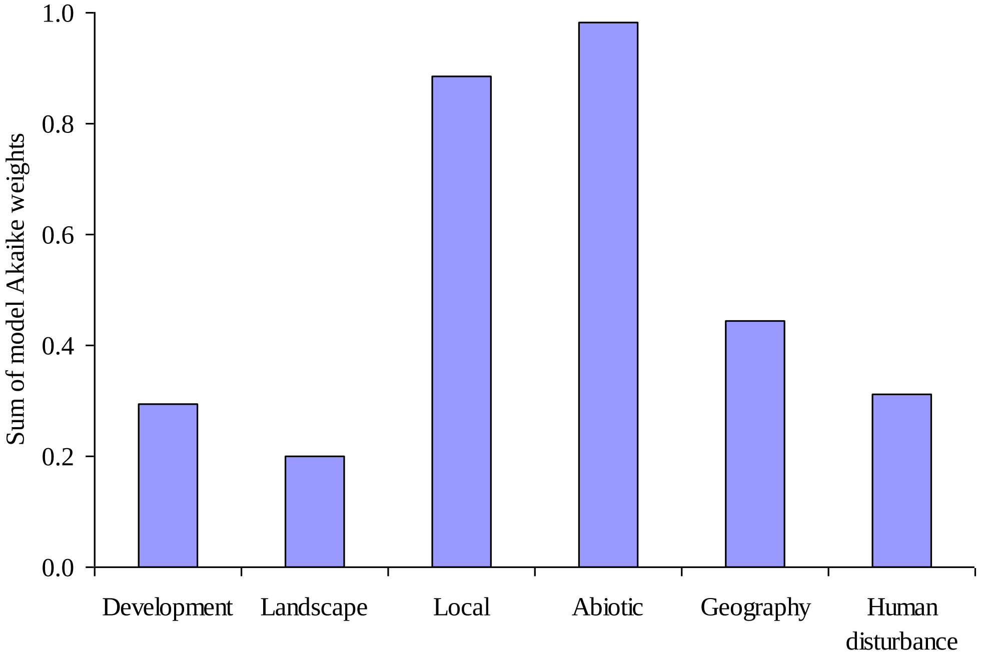


Figure 2.7. Association of six factor groups with abundance of invertivorous landbirds from 75 count stations in the Lake Tahoe basin, 2003-2004. Importance of each factor group is measured by summing the Akaike weights of models containing that factor group. See Table 2.2 for specific variables comprising each factor group.

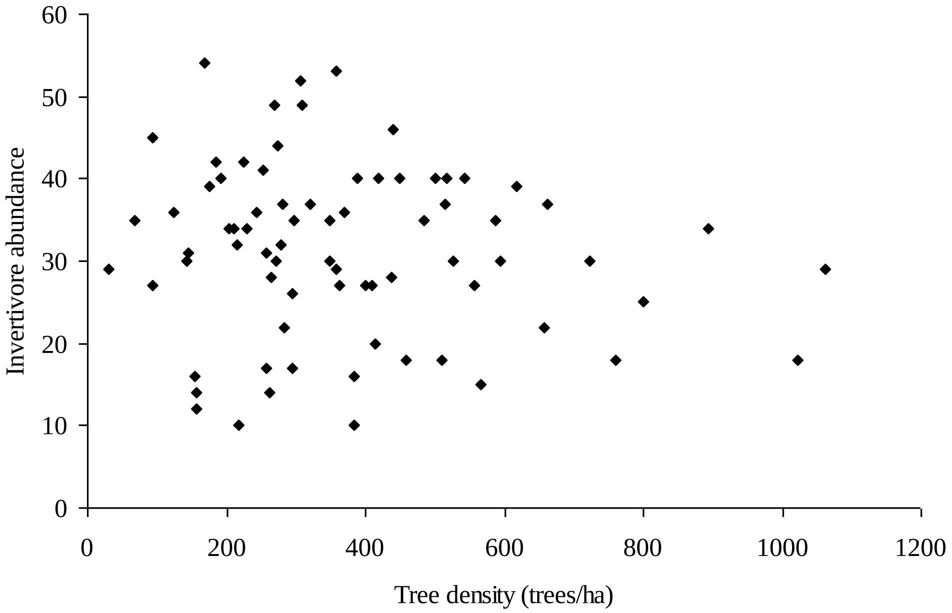


Figure 2.8. Abundance of invertivorous birds as a function of tree density at 75 sites along a gradient of urban development in the Lake Tahoe basin, 2003-2004.

Productivity

We located 671 active nests of 29 species (Table 2.10). Of these, we observed at least one interval for 566 nests of 28 species, and 10 species had sufficient numbers of observation intervals for nest survival analysis. However, nest-survival analyses were not possible for Northern Flicker and Red-breasted Nuthatch, which experienced one and zero failures, respectively.

Table 2.10. Numbers of active nests located, number with at least one observation interval, number of observation intervals available, predictor variables used in nest survival analyses, and number of candidate models for 10 species of landbirds targeted for nest monitoring along a development gradient in the Lake Tahoe basin, 2003-2005. Year and date were also included among candidate predictors when preliminary analysis showed it was warranted. Nest survival analysis could not be performed for Northern Flicker and Red-breasted Nuthatch because of miniscule to nonexistent failure rates, but we included the species in analyses of all cavity nesters and all species.

Target species	# nests	# nests with obs. int.	# obs. ints.	Predictors in nest survival analyses	# cand. models
Open nesters					
Dusky Flycatcher	20	19	78	Dev50,100,300	4
Steller's Jay	88	86	419	Substrate, dev50,100,300	16
American Robin	65	63	262	Nest ht, dev50,100,300	8
Dark-eyed Junco	51	47	126	Dev50,100,300	12
Western Wood-pewee	80	76	410	Nest ht, dev50,100,300	8
All open nesters (16 spp.)	330	310	1,346	Guild, dev50,100,300	16
Cavity nesters					
Mountain Chickadee	75	72	274	Substr., nest ht, dev50,100,300	16
Northern Flicker	45	24	139	N/A	N/A
Pygmy Nuthatch	58	50	239	Nest ht, dev50,100,300	16
Red-breasted Nuthatch	58	26	96	N/A	N/A
White-headed Woodpecker	31	31	187	Substr., nest ht, dev50,100,300	32
All cavity nesters (11 spp.)	341	256	1,077	Substrate, guild, dev50,100,300	20
TOTAL	671	566	2,423	Dev50,100,300	20

Analyses of nest daily survival rate (DSR) using the logistic-exposure method showed a variety of patterns of nest success in relation to explanatory variables such as development and substrate type (Appendix 2.3 and 2.4). For all species combined, the best time-specific model included year, with 55% of the weight of evidence, with year and date carrying 22% of the weight of evidence (Table 2.11a). DSR was lower in 2005 than in 2003 and 2004 (Fig. 2.9a). Year was included in further modeling involving all species. The best model generated in examining effects of nesting strategy (cavity or open), development, and year was a model with nest strategy and 300-m development (Table 2.11b), which showed higher overall success for cavity nesters, an overall increase in DSR with 300-m development, and a slightly greater increase for open nesters than for cavity nesters (Fig. 2.9a). Nesting strategy was present in all models with any weight, showing its overriding importance in determining DSR across species. Based on a 40-day nesting period (about average for the species in our study), cavity-nester nest success ranged from 74% at 0% development to 82% at 90% development, whereas open-nester nest success ranged from 40% success at 0% development to 55% at 90% development.

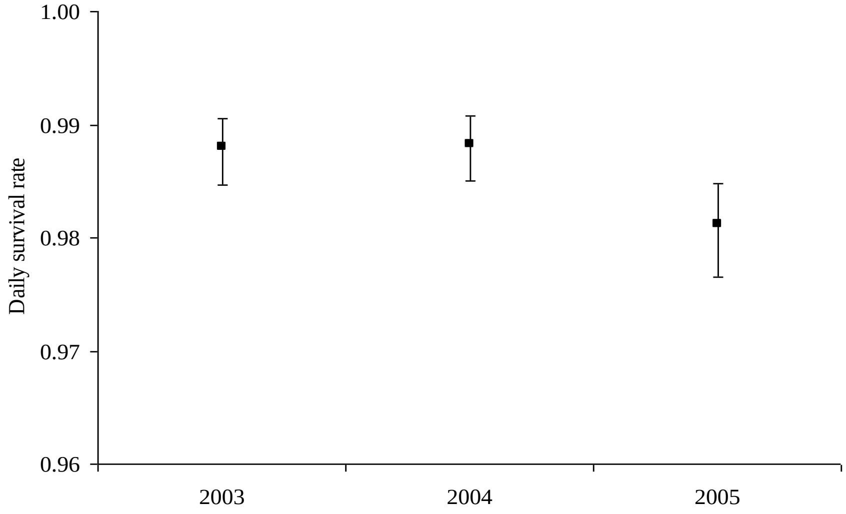
Table 2.11. Predictors of daily survival rates of nests of cavity nesters along a development gradient in the Lake Tahoe basin, 2003-2005.

a) Time-specific models for daily survival rate; the effective sample size was 9000.19, based on 2423 observation intervals for 566 nests.

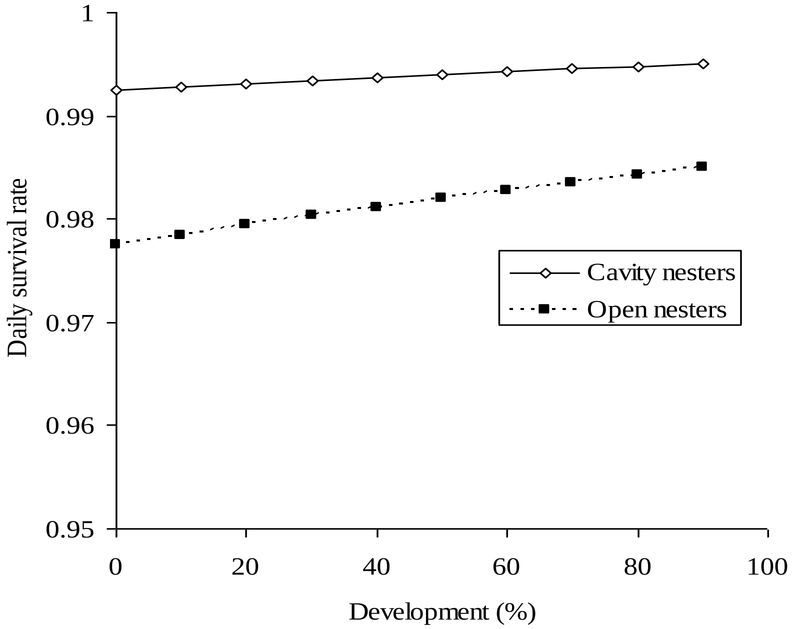
Model	K	AIC_c	ΔAIC_c	Weight
Year	3	986.82	0.00	0.547
Year, date	4	988.66	1.84	0.218
Year, date, $date^2$	5	989.64	2.81	0.134
Constant survival	1	991.42	4.60	0.055
Date, $date^2$	3	993.15	6.33	0.023
Date	2	993.21	6.39	0.022

b) Models totaling 80% of the weight of evidence for daily survival rate; the effective sample size was 9000.19, based on 2423 observation intervals for 566 nests.

Model	K	AIC_c	ΔAIC_c	Weight
Strategy, dev300	3	954.51	0.00	0.362
Strategy	2	956.19	1.68	0.156
Strategy, dev50	3	956.29	1.78	0.148
Strategy, year, strategy*year, dev300	7	957.82	3.31	0.069
Strategy, year, dev300	5	957.86	3.36	0.068



a) Daily survival rate for nests of all species along a development gradient in the Lake Tahoe basin, 2003-2005 (based on 2,423 observation intervals for 566 nests). Bars represent standard errors.



b) Cavity-nesting and open-nesting species (based on 1,346 observation intervals for 310 open nests and 1077 observation intervals for 256 cavity nests)

Figure 2.9. Daily survival rates for landbirds along a development gradient (percent developed within 300 m) in the Lake Tahoe basin, 2003-2005. .

For cavity nesters, the best time-specific model was the constant-survival model, with the year model next best (Table 2.12a). We did not include year as a potential predictor in further modeling because we were interested in modeling effects of two categorical predictors—guild and substrate. The best overall model was the constant-survival model, suggesting that development, guild (primary cavity excavator, weak cavity excavator, and secondary cavity nester), and substrate were weak influences on DSR. However, the constant-survival model carried only 26% of the weight, with development models next (Table 2.12b), so we plotted the slight decline in DSR with increasing 50-m development (Fig. 2.10). Nest success, based on an average 40-day nesting period, ranged from 73% to 78% along this gradient.

Table 2.12. Predictors of daily survival rates of nests of cavity nesters along a development gradient in the Lake Tahoe basin, 2003-2005.

a) Time-specific models for daily survival rates; the effective sample size was 4,167.14, based on 1,077 observation intervals for 256 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	243.65	0.00	0.426
Year	3	244.98	1.34	0.218
Date	2	245.57	1.92	0.163
year, date	4	246.93	3.28	0.083
date, $date^2$	3	247.17	3.52	0.073
year, date, $date^2$	5	248.52	4.87	0.037

b) Models totaling 80% of the weight of evidence for daily survival rate; the effective sample size was 4,167.14, based on 1,077 observation intervals for 256 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	243.65	0.00	0.262
dev50	2	244.17	0.52	0.202
dev300	2	244.78	1.13	0.149
dev100	2	245.54	1.89	0.102
substrate	3	246.74	3.09	0.056
substrate, dev300	4	247.30	3.65	0.042

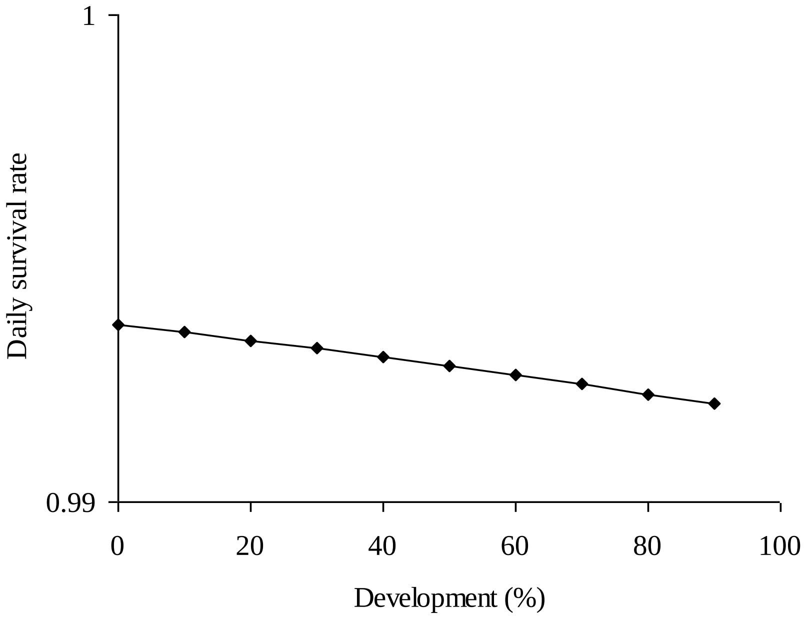


Figure 2.10. Daily survival rate for nests of cavity-nesting landbirds along a development gradient (percent developed within 50 m) in the Lake Tahoe basin, 2003-2005. Based on 1,077 observation intervals for 256 nests.

For open-nesters, seven observation intervals for three nests were omitted from analyses because they were the only ones associated with species nesting in the overstory. The best time-specific model was the constant-survival model, carrying 43% of the weight of evidence, with the date model carrying 26% (Table 2.13a). The model with date was considered in all future modeling. Overall models under consideration included guild (ground, tree, or shrub nesters) and development levels. Considerable model selection uncertainly existed, with the best overall model including guild and 50-m development, with 25% of the weight (Table 2.13b). DSR declined with 50-m development for all three nesting guilds, but was highest for understory tree nesters (Fig. 2.11). Based on an average 40-day nesting period, nest success ranged from 12% in shrubs in 90% development to 47% in trees in 0% development.

Table 2.13. Predictors of daily survival rates of nests of open nesters along a development gradient in the Lake Tahoe basin, 2003-2005.

a) Time-specific models for daily survival rate; the effective sample size was 4,800.09, based on 1,339 observation intervals for 307 nests.

Model	K	AIC$_c$	ΔAIC$_c$	Weight
constant survival	1	703.00	0.00	0.434
Date	2	704.06	1.06	0.255
Year	3	705.79	2.79	0.107
Date, date^2	3	705.87	2.87	0.103
Year, date	4	706.63	3.63	0.071

Year, date, date^2	5	708.32	5.33	0.030

b) Models totaling 80% of the weight of evidence for daily survival rate; the effective sample size was 4,800.09, based on 1,339 observation intervals for 307 nests.

Model	K	AIC$_c$	ΔAIC$_c$	Weight
guild, dev50	4	697.39	0.00	0.255
guild, date, dev50	5	698.50	1.11	0.146
guild, date	4	698.75	1.36	0.129
guild	3	698.91	1.52	0.119
guild, dev100	4	699.44	2.04	0.092
guild, date, dev100	5	700.06	2.67	0.067

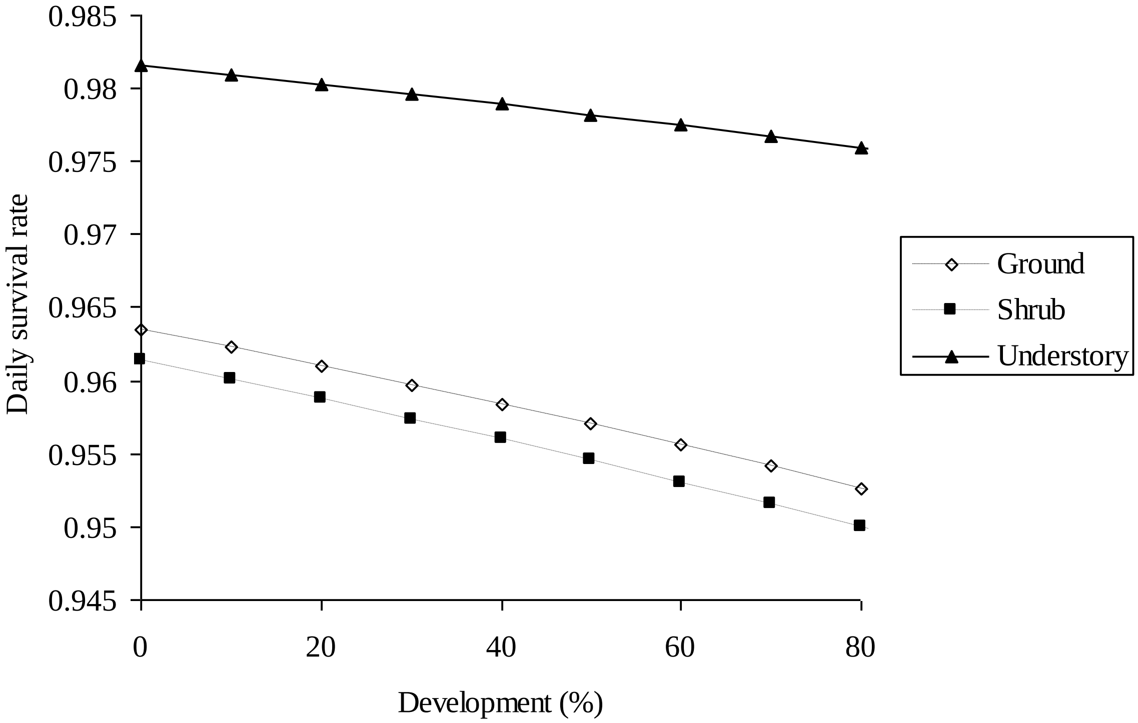


Figure 2.11. Daily survival rate for nests of open-nesting landbirds along a development gradient (percent developed within 50 m) in the Lake Tahoe basin, 2003-2005. Based on 1,339 observation intervals for 307 nests.

For Steller's Jay, the best time-specific model was the constant-survival model, which carried 51% of the weight of evidence (Table 2.11). The model with date carried 25% of the evidence; thus, date was included as a potential predictor in subsequent modeling. The best overall model was a linear effect of 50-m development and a categorical effect of nest substrate (either buildings or live trees; two nests in shrubs were omitted) (Table 2.12). Daily nest survival decreased with increasing development, and did so more for nests in trees than nests in buildings (Fig. 2.12). Nest success of jays, based on an average 36-day nesting period (Greene et al. 1998), ranged from 23% at 90% development to 65% at 0% development in trees and from 43% at 90% development to

72% at 20% development (approximately the lowest development level at which jays nested in buildings) in buildings.

Table 2.11. Time-specific models for daily survival rate of Steller's Jay nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 1717.47, based on 419 observation intervals for 86 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	247.56	0.00	0.515
Date	2	248.96	1.39	0.257
date, date^2	3	250.70	3.13	0.107
Year	3	251.53	3.97	0.071
year, date	4	252.92	5.36	0.035
year, date, date^2	5	254.67	7.10	0.015

Table 2.12. Models totaling 80% of the weight of evidence for daily survival rate of Steller's Jay nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 1688.23, based on 413 observation intervals for 84 nests.

Model	K	AIC_c	ΔAIC_c	Weight
substrate, dev50	3	234.92	0.00	0.206
substrate, dev50, dev50^2	4	235.90	0.99	0.126
substrate, dev100	3	236.21	1.30	0.108
substrate, dev50, date	4	236.87	1.96	0.078
dev50	2	237.25	2.33	0.064
substrate, dev100, dev100^2	4	237.31	2.39	0.063
dev100, dev100^2	3	237.74	2.82	0.050
substrate, dev5, dev50^2, date	5	237.84	2.92	0.048
substrate, dev100, date	4	238.01	3.09	0.044
dev100	2	238.81	3.89	0.030

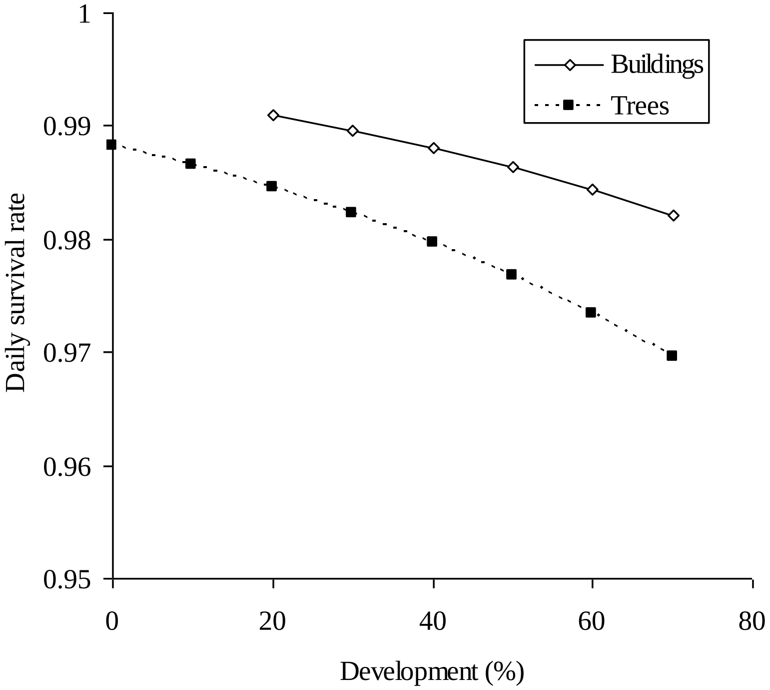


Figure 2.12. Daily survival rate for Steller's Jay nests in buildings and in trees along a development gradient (percent developed within 50 m) in the Lake Tahoe basin, 2003-2005. Only the range of development values over which jays were found nesting in each substrate type is depicted. Based on 209 observation intervals for 37 nests in buildings, and 204 observation intervals for 47 nests in trees.

For Mountain Chickadees, the best time-specific model was again the constant-survival model, carrying 46% of the weight of evidence (Table 2.13). Both the year model and the date model had 17% of the weight, but neither explained much of the variation in DSR, thus they were not carried forward. The best overall model, but weakly so, was the constant-survival model, with 27% of the weight (Table 2.14). The model containing only 300-m development carried 17% of the weight, but there was essentially no relationship between development and DSR (Fig. 2.13). Mountain Chickadees had relatively high nest success based on an average 43.5-day nesting period (McCallum et al. 1999), ranging from 59% to 70%.

Table 2.13. Time-specific models for daily survival rate of Mountain Chickadee nests along a development gradient in the Lake Tahoe basin, 2003-2004. The effective sample size was 965.45, based on 274 observation intervals for 72 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	93.63	0.00	0.457
Year	2	95.62	1.99	0.169
Date	2	95.63	2.00	0.168
Date, date^2	3	96.60	2.97	0.104
Year, date	3	97.59	3.96	0.063
Year, date, date^2	4	98.58	4.95	0.039

Table 2.14. Models totaling over 80% of the weight of evidence for daily survival rate of Mountain Chickadee nests along a development gradient in the Lake Tahoe basin, 2003-2004. The effective sample size was 965.45, based on 274 observation intervals for 72 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	93.63	0.00	0.267
Dev300	2	94.57	0.94	0.167
Nest_ht	2	94.96	1.33	0.137
Dev100	2	95.49	1.86	0.105
Dev50	2	95.64	2.01	0.098
Nest_ht, dev300	3	95.80	2.17	0.090

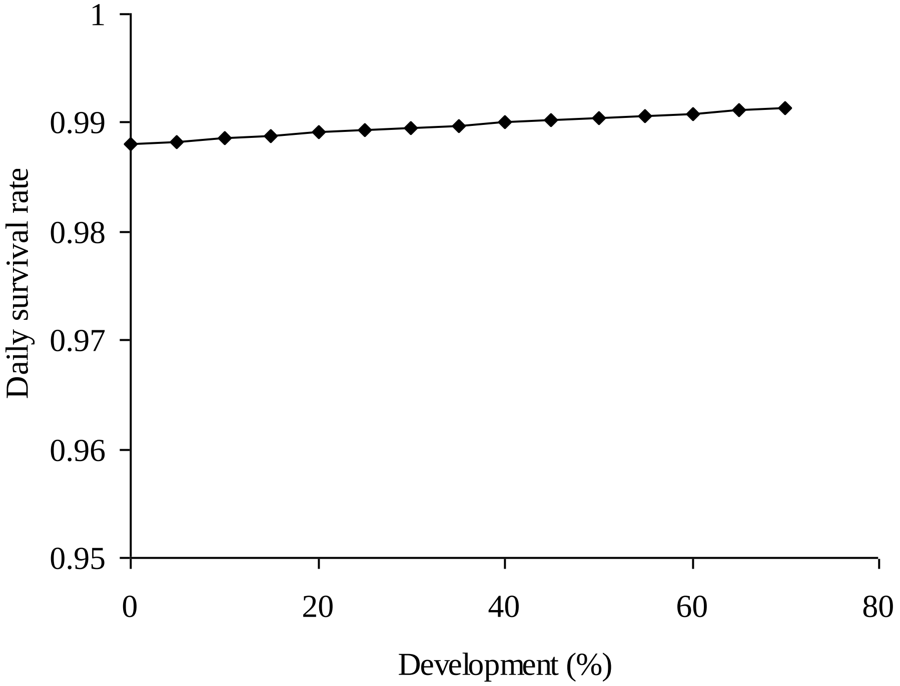


Figure 2.13. Daily survival rate for Mountain Chickadee nests along a development gradient (percent developed within 300 m) in the Lake Tahoe basin, 2003-2004. Only the range of development values in which chickadees were found nesting is depicted. Nest height was held constant. Based on 274 observation intervals for 72 nests.

For Dark-eyed Juncos, the best time-specific model included year only, carrying 47% of the weight of evidence (Table 2.15). The model with year and date, carrying 21% of the weight of evidence, was also carried forward for consideration in further modeling. The best overall model included year and 50-m development (Table 2.16). DSR decreased with increasing development and was substantially lower in 2004 than in other years (Fig. 2.14). Nest success of juncos based on an average 26.5-day nesting period (Nolan Jr. et al. 2002) ranged from 79% in 0% development in 2005 to only 1% in 90% development in 2004.

Table 2.15. Time-specific models for daily survival rate of Dark-eyed Junco nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 386.73, based on 126 observation intervals for 47 nests.

Model	K	AIC$_c$	ΔAIC$_c$	Weight
Year	3	83.98	0.00	0.473
Year, date	4	85.64	1.67	0.205
constant survival	1	86.16	2.19	0.158
year, date, date^2	5	87.51	3.53	0.081
Date	2	88.08	4.10	0.061
date, date^2	3	90.08	6.10	0.022

Table 2.16. Models totaling over 80% of the weight of evidence for daily survival rate of Dark-eyed Junco nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 386.73, based on 126 observation intervals for 47 nests.

Model	K	AIC$_c$	ΔAIC$_c$	Weight
year, dev50	4	82.59	0.00	0.293
Year	3	83.98	1.39	0.146
year, date, dev50	5	84.19	1.60	0.132
year, dev300	4	84.58	1.99	0.108
year, dev100	4	85.53	2.94	0.067
year, date	4	85.64	3.06	0.064

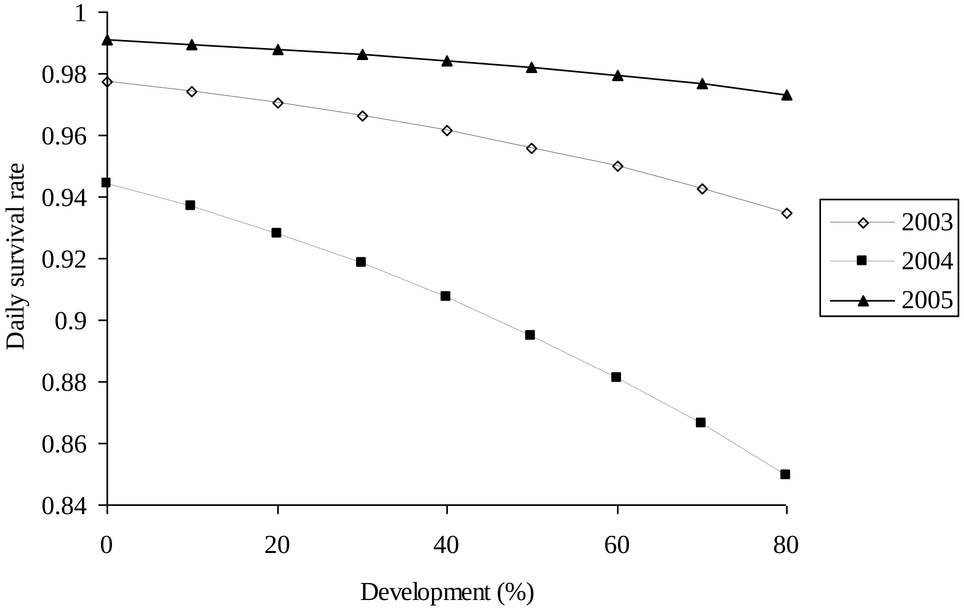


Figure 2.14. Daily survival rate for Dark-eyed Junco nests in each of three years along a development gradient (percent developed within 50 m) in the Lake Tahoe basin. Only the range of development values in which juncos were found nesting is depicted. Based on 38 observation intervals for 12 nests in 2003, 28 intervals for 12 nests in 2004, and 60 intervals for 23 nests in 2005.

For Dusky Flycatchers, the best time-specific model was the constant-survival model, carrying 51% of the weight of evidence (Table 2.17). The model with date carried 21% of the weight of evidence and was considered in future modeling. The best overall model, although there was substantial model selection uncertainty, included only 100-m development (Table 2.18), which had a positive relationship with DSR (Fig. 2.15). Dusky Flycatcher nests were found only at 100-m development values of 5.62 and lower. Their nest success was low overall; based on an average 36.5-day nesting period (Sedgwick 1993) ranged from 18% at 0% development to 53% at 6% development.

Table 2.17. Time-specific models for daily survival rate of Dusky Flycatcher nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 254.71, based on 78 observation intervals for 19 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	57.75	0.00	0.507
Date	2	59.56	1.80	0.206
Year	3	60.69	2.94	0.117
Date, date^2	3	61.14	3.38	0.093
Year, date	4	62.39	4.63	0.050
Year, date, date^2	5	63.64	5.89	0.027

Table 2.18. Models for daily survival rate of Dusky Flycatcher nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 254.71, based on 78 observation intervals for 19 nests.

Model	K	AIC_c	ΔAIC_c	Weight
dev100	2	56.93	0.00	0.427
constant survival	1	57.75	0.82	0.283
dev50	2	58.93	2.00	0.157
dev300	2	59.27	2.34	0.132

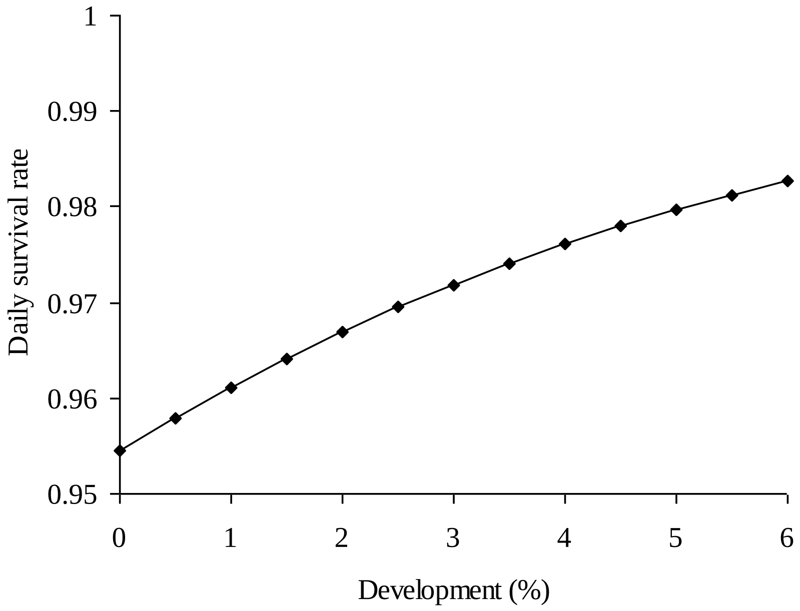


Figure 2.15. Daily survival rate for Dusky Flycatcher nests along a development gradient (percent developed within 100 m) in the Lake Tahoe basin, 2003-2005. Only the range of development values in which flycatchers were found nesting is depicted. Based on 78 observation intervals for 19 nests.

For Pygmy Nuthatches, the best time-specific model was the constant-survival model, with 35% of the weight, followed by the year model, with 30% of the weight (Table 2.19). As a result, year was included as a candidate predictor in further modeling. We located insufficient numbers of nests in alternative substrates (i.e., other than snags; buildings and other structures, n = 3, live trees, n = 4) to model effects of substrate. The best overall model included year, 50-m development, and nest height (Table 2.20). DSR dropped precipitously with development in 2003 but was constant with development in 2004 (Fig. 2.16). Nest success based on an average 40-day nesting period (Kingery and Ghalambor 2001) ranged from 100% in 0% development in 2004 to <1% in 80% development in 2003.

Table 2.19. Time-specific models for daily survival rate of Pygmy Nuthatch nests along a development gradient in the Lake Tahoe basin, 2003-2004. The effective sample size was 914.55, based on 239 observation intervals for 50 nests.

Model	K	AIC$_c$	ΔAIC$_c$	Weight
constant survival	1	41.07	0.00	0.350
year	2	41.36	0.30	0.302
date	2	42.94	1.87	0.137
year, date	3	43.30	2.23	0.115
date, date^2	3	44.87	3.80	0.052
year, date, date^2	4	45.27	4.20	0.043

Table 2.20. Models accounting for 80% of the weight of evidence for daily survival rate of Pygmy Nuthatch nests along a development gradient in the Lake Tahoe basin, 2003-2004. The effective sample size was 914.55, based on 239 observation intervals for 50 nests.

Model	K	AIC$_c$	ΔAIC$_c$	Weight
year, dev50, nest_ht	4	30.56	0.00	0.497
year and dev50	3	31.22	0.67	0.356

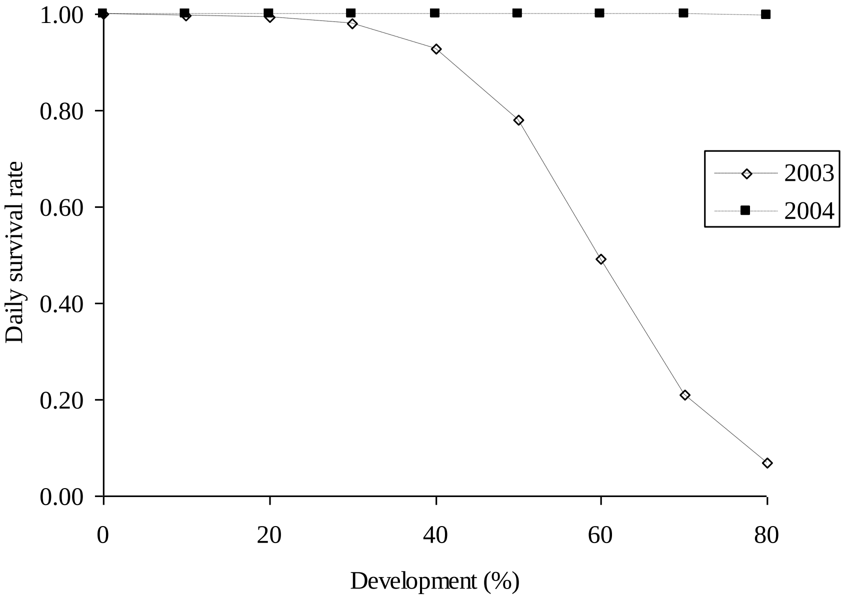


Figure 2.16. Daily survival rate for Pygmy Nuthatch nests along a development gradient (percent developed within 50 m) in the Lake Tahoe basin, 2003-2004. Only the range of development values in which nuthatches were found nesting is depicted. Nest height was held constant for this depiction. Based on 239 observation intervals for 50 nests.

For American Robin, the best time-specific model was the constant-survival model, carrying 39% of the weight of evidence (Table 2.21). The year model and date model each carried some weight but effects of date and year were weak and were omitted from consideration in further modeling. The best overall model was the constant-survival model, carrying 28% of the weight of evidence (Table 2.22). There was no obvious relationship between DSR and development or nest height.

Table 2.21. Time-specific models for daily survival rate of American Robin nests along a development gradient in the Lake Tahoe basin, 2003-2004. The effective sample size was 890.32, based on 262 observation intervals for 63 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	107.97	0.00	0.388
Year	2	109.35	1.39	0.194
Date	2	109.49	1.52	0.181
Year, date	3	110.28	2.31	0.122
Date, $date^2$	3	111.43	3.46	0.069
Year, date, $date^2$	4	112.24	4.27	0.046

Table 2.22. Models accounting for 80% of the weight of evidence for daily survival rate of American Robin nests along a development gradient in the Lake Tahoe basin, 2003-2004. The effective sample size was 890.32, based on 262 observation intervals for 63 nests.

Model	K	AIC_c	ΔAIC_c	Weight
constant survival	1	107.97	0.00	0.275
Nest_ht	2	109.30	1.33	0.142
Dev300	2	109.39	1.43	0.135

Dev100	2	109.42	1.46	0.133
Dev50	2	109.80	1.84	0.110
Nest_ht, dev100	3	110.53	2.57	0.076

For White-headed Woodpecker, the best time-specific models were the year model and the constant-survival model, both with 28% of the weight of evidence (Table 2.23); each was retained for consideration in further modeling. Two nests in human structures, accounting for six observation intervals, were omitted. The interaction between year and substrate (live trees vs. snags and logs) could not be examined, as no live trees were used in 2003. Considerable model selection uncertainty existed in finding an overall best model. The model with year and 300-m development was the best model, but carried only 10% of the weight of evidence (Table 2.24). DSR increased with 300-m development but this relationship varied by year (Fig. 2.17). Success was high overall; there were no nest failures in 2003 and only one in 2004. Success rates based on an average 44.5-day nesting period (Garrett et al. 1996) ranged from 50% in 0% development in 2005 to 100% in all levels of development in 2003.

Table 2.23. Time-specific models for daily survival rate of White-headed Woodpecker nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 658.71, based on 187 observation intervals for 31 nests.

Model	K	AIC_c	ΔAIC_c	Weight
year	3	54.62	0.00	0.283
constant survival	1	54.68	0.06	0.275
date	2	56.34	1.71	0.120
year, date, $date^2$	5	56.37	1.75	0.118
year, date	4	56.43	1.81	0.115
date, $date^2$	3	56.95	2.33	0.088

Table 2.24. Models accounting for 80% of the weight of evidence for daily survival rate of White-headed Woodpecker nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 658.71, based on 181 observation intervals for 29 nests.

Model	K	AIC_c	ΔAIC_c	Weight
year, dev300	4	53.36	0.00	0.103
year	3	53.93	0.57	0.077
nest_ht	2	54.02	0.66	0.074
constant survival	1	54.14	0.78	0.069
year, nest_ht	4	54.85	1.49	0.049
year, dev300, nest_ht	5	54.88	1.53	0.048
substrate, year, dev300	5	55.17	1.81	0.042
year, dev100	4	55.34	1.98	0.038
dev300	2	55.46	2.10	0.036
nest_ht, dev300	3	55.54	2.18	0.034
year, dev50	4	55.68	2.32	0.032
substrate	2	55.72	2.36	0.032
substrate, nest_ht	3	55.74	2.39	0.031
substrate, year	4	55.96	2.60	0.028
nest_ht, dev50	3	56.00	2.64	0.027
nest_ht, dev100	3	56.02	2.66	0.027
dev100	2	56.11	2.76	0.026

Model	K	AIC$_c$	ΔAIC$_c$	Weight
dev50	2	56.15	2.79	0.025

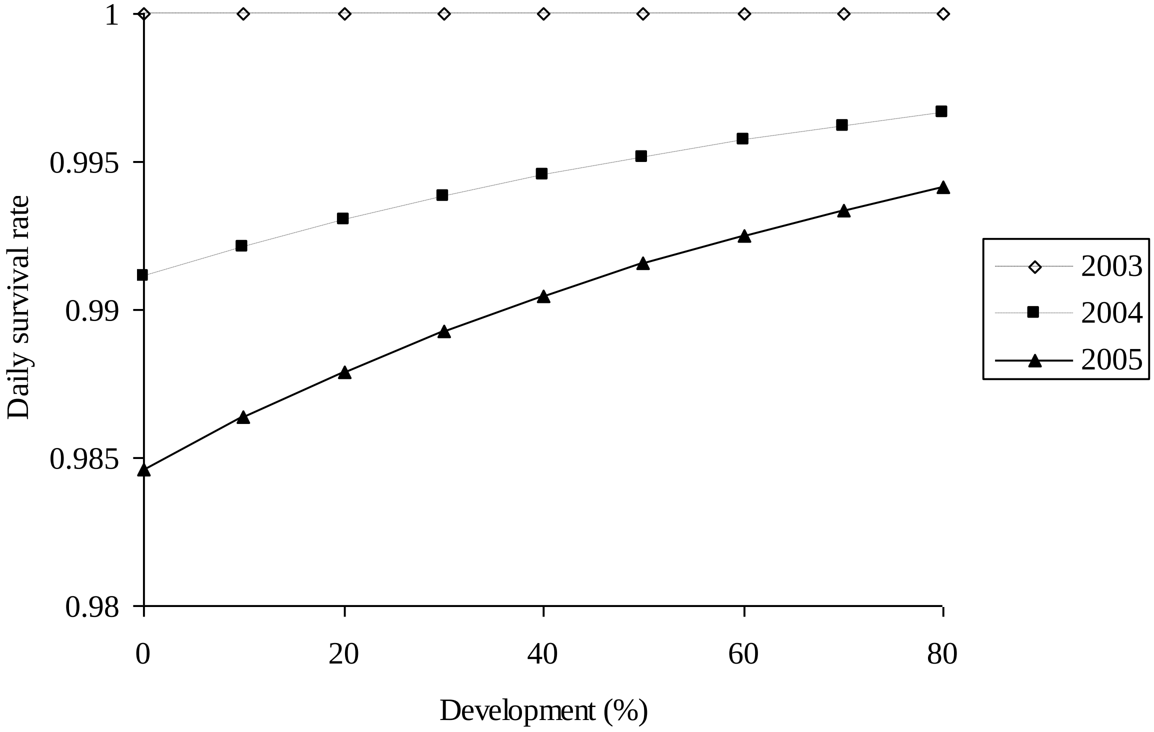


Figure 2.17. Daily survival rate for White-headed Woodpecker nests along a development gradient (percent developed within 100 m) in the Lake Tahoe basin, 2003-2005. Based on 181 observation intervals for 29 nests.

For Western Wood-pewees, the best time-specific model was the constant-survival model, with over 40% of the weight (Table 2.25). Models with date and year were not considered in further modeling. The best overall model, although considerable model selection uncertainty existed, was nest height, with 26% of the weight of evidence. DSR increased with increasing nest height (Fig. 2.18). Nest success based on an average 34-day nesting period (Bemis and Rising 1999) ranged from 49% at 2 m to 79% at 18 m.

Table 2.25. Time-specific models for daily survival rate of Western Wood-pewee nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 1,374.21, based on 410 observation intervals for 76 nests.

Model	K	AIC$_c$	ΔAIC$_c$	Weight
constant survival	1	164.36	0.00	0.405
date	2	165.99	1.62	0.180
year	3	166.06	1.69	0.174
date, date^2	3	167.10	2.74	0.103
year, date	4	167.52	3.16	0.083
year, date, date^2	5	168.36	3.99	0.055

Table 2.26. Models accounting for 80% of the weight of evidence for daily survival rate of Western Wood-pewee nests along a development gradient in the Lake Tahoe basin, 2003-2005. The effective sample size was 1,374.21, based on 410 observation intervals for 76 nests.

Model	K	AIC_c	ΔAIC_c	Weight
nest_ht	2	163.38	0.00	0.259
constant survival	1	164.00	0.63	0.189
nest_ht, dev100	3	165.00	1.63	0.115
nest_ht, dev50	3	165.12	1.74	0.108
nest_ht, dev300	3	165.37	1.99	0.096
dev100	2	165.70	2.32	0.081

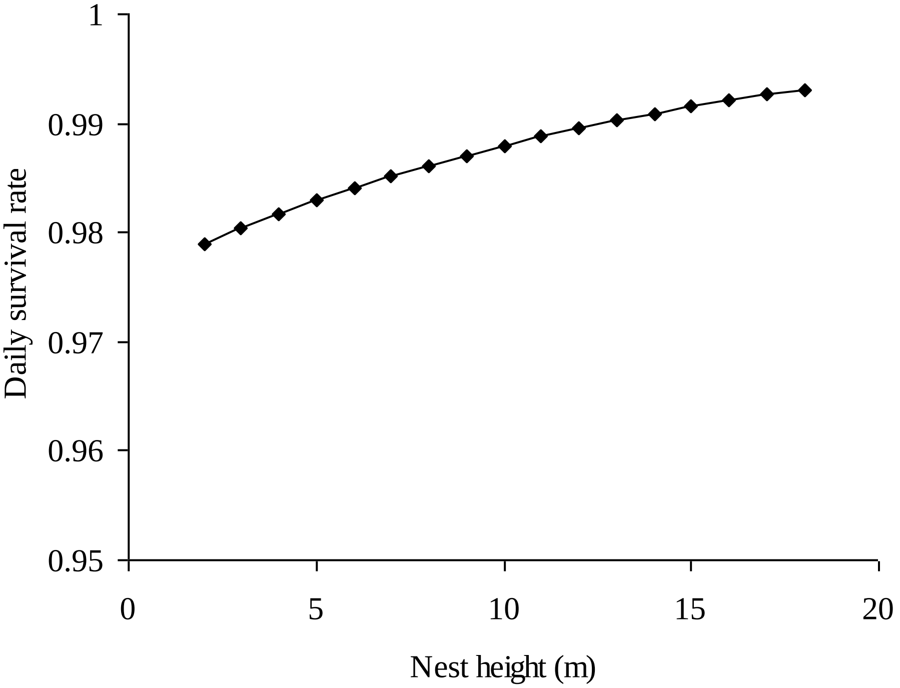


Figure 2.18. Daily survival rate for Western Wood-pewee nests along a development gradient in the Lake Tahoe basin in relation to nest height, 2003-2005. Only the range of nest heights used is depicted. Based on 410 observation intervals for 76 nests.

Abundance

Individual species varied widely in their responses to urbanization. Over one-half of the 67 native species in the sample showed a significant ($P < 0.05$) association with 300-m development: 14 species (21%) increased significantly in abundance and 25 species (37%) decreased (Table 2.27). Twenty-eight species showed no significant relationship to development, including the common Mountain Chickadee, Northern Flicker, Pine Siskin, and Cassin’s Finch.

Table 2.27. Frequency of occurrence (proportion of sites with presence) of 67 native landbird species and Pearson's correlation with percent development within 300 m of 375 point count stations in the Lake Tahoe basin, 2003-2004. Those species listed as decreasing or increasing have significant correlations with development ($P < 0.05$).

Species	Freq.	r	Species	Freq.	r	Species	Freq.	r
Decreasing with development			*Neutral*			*Increasing with development*		
Dusky Flycatcher	0.25	-0.521	Common Nighthawk	0.01	-0.093	American Crow	0.01	0.111
Red-breasted Nuthatch	0.61	-0.463	Calliope Hummingbird	0.01	-0.084	Lesser Goldfinch	0.01	0.120
Western Tanager	0.68	-0.429	Evening Grosbeak	0.57	-0.082	Tree Swallow	0.03	0.136
Yellow-rumped Warbler	0.72	-0.387	Spotted Towhee	0.15	-0.080	Black-headed Grosbeak	0.15	0.166
Brown Creeper	0.55	-0.375	Mountain Chickadee	0.99	-0.076	Common Raven	0.13	0.177
Nashville Warbler	0.21	-0.368	Purple Finch	0.02	-0.075	Barn Swallow	0.05	0.195
Townsend's Solitaire	0.17	-0.357	Pine Grosbeak	0.02	-0.071	Cliff Swallow	0.19	0.196
Hairy Woodpecker	0.38	-0.352	Lincoln's Sparrow	0.00	-0.065	Band-tailed Pigeon	0.27	0.199
Hermit Thrush	0.11	-0.346	Black-billed Magpie	0.00	-0.065	Mourning Dove	0.51	0.237
Fox Sparrow	0.54	-0.328	Savannah Sparrow	0.00	-0.065	Pygmy Nuthatch	0.67	0.312
Cassin's Vireo	0.13	-0.294	Rufous Hummingbird	0.00	-0.053	Brown-headed Cowbird	0.84	0.334
Olive-sided Flycatcher	0.22	-0.276	Green-tailed Towhee	0.03	-0.041	American Robin	0.84	0.388
Golden-crowned Kinglet	0.16	-0.274	Cassin's Finch	0.19	-0.038	Brewer's Blackbird	0.41	0.411
White-breasted Nuthatch	0.36	-0.272	Clark's Nutcracker	0.19	-0.025	Steller's Jay	0.99	0.593
Dark-eyed Junco	0.83	-0.264	Yellow Warbler	0.01	-0.008			
Warbling Vireo	0.18	-0.236	Pine Siskin	0.31	-0.005			
Western Wood-pewee	0.47	-0.221	Blue Grouse	0.00	-0.003			
Mountain Quail	0.06	-0.219	Song Sparrow	0.07	0.008			
Hermit Warbler	0.04	-0.209	House Wren	0.04	0.019			
Wilson's Warbler	0.07	-0.180	Red-winged Blackbird	0.06	0.022			
Pileated Woodpecker	0.03	-0.164	House Finch	0.00	0.029			
Chipping Sparrow	0.06	-0.154	Red-breasted Sapsucker	0.08	0.030			
Williamson's Sapsucker	0.04	-0.152	Northern Flicker	0.55	0.030			
MacGillivray's Warbler	0.15	-0.133	Downy Woodpecker	0.07	0.037			
Black-backed Woodpecker	0.01	-0.107	Bushtit	0.00	0.038			
			Red Crossbill	0.06	0.041			
			Yellow-headed Blackbird	0.01	0.042			
			White-headed Woodpecker	0.40	0.065			

Associated positively with development were previously identified synanthropic species like Steller's Jays, American Robins, and Brown-headed Cowbirds, as well as Cliff Swallows and Brewer's Blackbirds. (Although exotic species were not a focus of this analysis, there were four in the dataset: European Starling, House Sparrow, Rock Pigeon, and California Quail. Each was more abundant with increasing development.) A closer look revealed several of these positive relationships to be unimodal (see 2004 report), with low abundance at the extremes of the gradient and the highest abundance at the middle or in high but not the highest development. Twenty-five species declined with urbanization, including species expected to be less abundant in urbanized areas, such as the old-growth dependent Pileated Woodpecker, and species not previously expected to show such a pattern, such as the Dusky Flycatcher and Brown Creeper. Future analyses will focus on whether such declines are the result of missing habitat elements, human use, or for some species, nest success.

Habitat Use: Nest-site Selection

Nest height

The best models using number of people encountered per hour as a measure of human use and development at three scales varied by species and species group (Table 2.28). We were able to generate reasonable models to explain nest height for all primary cavity nesters, American Robin, Northern Flicker, Red-breasted Nuthatch, White-breasted Nuthatch, and Western Wood-pewee. Nest heights for the remainder of species groups and individual species showed very weak, if any, associations with development and human use. As one example, nest heights of all primary cavity nesters decreased with increasing 100-m development (Fig. 2.20).

Table 2.28. Models totaling 80% of the weight of evidence in explaining nest height with development and human use for three species groups and nine individual species. Data were collected in the Lake Tahoe basin, 2003-2005.

Variables in model	AIC_c	ΔAIC_c	Weight	Adj. R^2
All primary cavity nesters (n = 67 nests)				
Dev100	146.72	0.00	0.229	0.050
Dev50	147.19	0.47	0.181	0.043
Dev100,300	148.51	1.80	0.093	0.042
Dev50,100	148.94	2.22	0.075	0.036
People, Dev100	148.99	2.27	0.074	0.035
People, Dev50	149.25	2.53	0.065	0.031
Dev50,300	149.43	2.72	0.059	0.028
Dev300	149.81	3.10	0.049	0.004
All weak cavity excavators and secondary cavity nesters (n = 156 nests)				
Dev50	377.27	0.00	0.156	-0.004
Dev300	377.36	0.09	0.149	-0.005
Dev100	377.40	0.14	0.146	-0.005
People	377.45	0.18	0.142	-0.005
Dev50,100	379.32	2.06	0.056	-0.010
Dev50,300	379.35	2.08	0.055	-0.011
People, Dev50	379.35	2.09	0.055	-0.011
Dev100,300	379.46	2.19	0.052	-0.011

Variables in model	AIC$_c$	ΔAIC$_c$	Weight	Adj. R^2
All understory tree nesters (n = 158 nests)				
People, Dev300	258.22	0.00	0.271	0.027
People, Dev50,300	260.18	1.96	0.102	0.022
People, Dev100,300	260.25	2.03	0.098	0.021
People, Dev50,100,300	260.35	2.13	0.093	0.028
Dev300	260.52	2.30	0.086	0.006
Dev50	261.65	3.43	0.049	-0.001
Dev50,100,300	261.97	3.75	0.042	0.010
Dev100,300	262.01	3.79	0.041	0.003
People	262.01	3.79	0.041	-0.004
American Robin (n = 49 nests)				
People, Dev300	91.29	0.00	0.138	0.069
People, Dev50,300	91.63	0.34	0.116	0.089
People, Dev100,300	91.64	0.35	0.116	0.089
Dev100,300	91.88	0.59	0.103	0.057
Dev50,300	92.01	0.72	0.096	0.055
People	92.14	0.85	0.090	0.026
Dev50	92.33	1.04	0.082	0.023
Dev100	93.25	1.96	0.052	0.004
People, Dev50	94.04	2.75	0.035	0.015
Mountain Chickadee (n = 45 nests)				
Dev100	95.54	0.00	0.185	0.026
People	96.04	0.50	0.144	0.015
Dev300	96.08	0.53	0.141	0.015
Dev50	96.50	0.95	0.115	0.005
Dev50,100	97.27	1.72	0.078	0.018
People, Dev100	97.79	2.25	0.060	0.007
Dev100,300	97.96	2.41	0.055	0.003
People, Dev50	98.26	2.71	0.048	-0.004
Northern Flicker (n = 28 nests)				
People	42.50	0.00	0.187	0.102
Dev100	43.01	0.51	0.145	0.085
Dev50	43.71	1.21	0.102	0.062
Dev100,300	43.72	1.22	0.102	0.115
People, Dev300	44.15	1.66	0.082	0.101
People, Dev100,300	44.41	1.91	0.072	0.151
People, Dev50	44.63	2.14	0.064	0.086
People, Dev100	44.67	2.18	0.063	0.084
Pygmy Nuthatch (n = 50 nests)				
People	106.53	0.00	0.216	0.014
Dev100	107.41	0.88	0.139	-0.003
Dev300	107.71	1.19	0.119	-0.010
Dev50	107.72	1.20	0.119	-0.010
People, Dev100	108.83	2.30	0.068	-0.006

Variables in model	AIC_c	ΔAIC_c	Weight	Adj. R^2
People, Dev50	108.86	2.33	0.067	-0.006
People, Dev300	108.89	2.36	0.066	-0.007
Dev50,100	109.74	3.21	0.043	-0.024
Red-breasted Nuthatch (n = 40 nests)				
Dev50	60.37	0.00	0.238	0.117
Dev100	61.50	1.13	0.135	0.091
Dev50,300	61.90	1.53	0.111	0.114
Dev100,300	61.97	1.60	0.107	0.112
People, Dev50	62.27	1.90	0.092	0.106
Dev50,100	62.83	2.45	0.070	0.093
People, Dev100	62.89	2.52	0.067	0.092
Steller's Jay (n = 61 nests)				
People	95.03	0.00	0.179	0.024
People, Dev300	95.20	0.17	0.164	0.041
People, Dev100	95.21	0.17	0.164	0.041
People, Dev50	96.58	1.54	0.083	0.019
People, Dev50,100	97.11	2.08	0.063	0.031
People, Dev100,300	97.14	2.11	0.062	0.031
People, Dev50,300	97.43	2.40	0.054	0.026
Dev300	97.48	2.45	0.052	-0.016
White-breasted Nuthatch (n = 18 nests)				
People, Dev50,300	15.82	0.00	0.654	0.636
Dev50,300	18.68	2.86	0.156	0.504
Western Wood-pewee (n = 44 nests)				
People, Dev50,100,300	40.60	0.00	0.357	0.193
Dev50,100,300	43.08	2.48	0.103	0.113
People	43.12	2.53	0.101	0.051
People, Dev300	43.73	3.14	0.074	0.068
Dev50,100	43.93	3.33	0.068	0.063
People, Dev100,300	44.14	3.55	0.061	0.091
People, Dev50,100	44.72	4.12	0.046	0.078
White-headed Woodpecker (n = 18 nests)				
Dev50	22.39	0.00	0.210	-0.009
People	22.77	0.38	0.174	-0.030
Dev100	22.99	0.61	0.155	-0.044
Dev300	23.27	0.88	0.135	-0.060
People, Dev50	24.92	2.54	0.059	-0.028
Dev50,100	24.98	2.59	0.058	-0.031
Dev50,300	25.25	2.86	0.050	-0.047

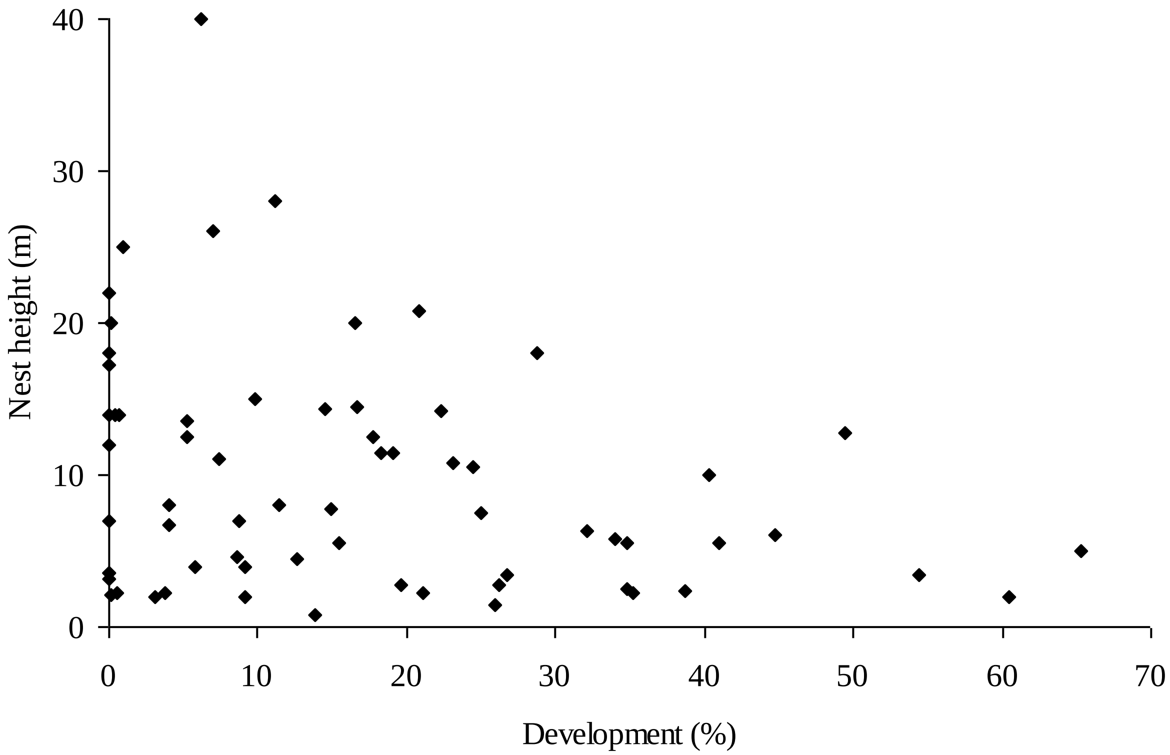


Figure 2.20. Nest heights of primary cavity nesters in relation to percent development within 100 m of 67 nests in the Lake Tahoe basin, 2003-2005.

Nest substrate

Primary cavity excavators used dead substrates with nearly equal frequencies in low (75% of 44 nests) and high (74% of 43 nests) development, as opposed to live substrates (χ^2 = 0.004, *P* = 0.950). However, six nests of primary cavity excavators in human structures, which were excluded from the analysis, were all in high development. Weak cavity excavators and secondary cavity nesters used human structures more frequently in high (20% of 104 nests) than in low (2% of 130 nests) development and tended to use dead substrates more often in low development (85% of nests) than in high development (68% of nests) but the proportion of nests in live substrates remained essentially the same in the two development categories (χ^2 = 25.129, *P* < 0.001). Mountain Chickadees appeared to use more dead substrates in high development (90% of 42 nests) than in low development (75% of 24 nests), as opposed to live substrates, but the difference was only marginally significant (χ^2 = 2.734, *P* = 0.098). In addition, nine chickadee nests in human structures were excluded from the analysis: one in low development and eight in high development. Northern Flickers used dead substrates with roughly equal frequencies in low (84% of 25 nests) and high (75% of 16 nests) development, as opposed to live substrates (χ^2 = 2.734, *P* = 0.098). Four flicker nests in human structures, all in high development, were excluded from analysis. Pygmy Nuthatches used dead substrates with roughly equal frequencies in low (93% of 29 nests) and high (88% of 33 nests) development, as opposed to live substrates (χ^2 = 0.493, *P* = 0.483). Seven Pygmy Nuthatch nests in human structures, all in high development, were excluded from analysis. Steller's Jays used human structures more often in high (56% of 55 nests) than in low (19% of 31 nests) development, as opposed to live trees and shrubs ($\chi^2 = 11.726$, $P = 0.001$). White-breasted Nuthatches used dead substrates with roughly equal frequencies in low (62% of 13 nests) and high (50% of 8 nests) development, as opposed to live substrates ($\chi^2 = 0.269$, $P = 0.604$). Seven White-breasted Nuthatch nests in human structures—six in high development and one in low development—were excluded from analysis. White-headed Woodpecker used dead substrates with roughly equal frequencies in low (81% of 16 nests) and high (69% of 13 nests) development, as opposed to live substrates ($\chi^2 = 0.564$, $P = 0.453$). Two woodpecker nests in human structures in high development were excluded from analysis.

Habitat Use: Foraging

In 2003 and 2004 we conducted 793 behavioral observations. We observed foraging in 663 of these observations, involving 19 species. All analyses were conducted on this subset of 663 foraging observations. The species with the most observations were Steller's Jay (n = 177), Mountain Chickadee (n = 152), American Robin (n = 60), Dark-eyed Junco (n = 53), Pygmy Nuthatch (n = 43), White-headed Woodpecker (n = 39), Hairy Woodpecker (n = 30), and Red-breasted Nuthatch (n = 25).

Across all species, birds foraged lower to the ground in high development ($\chi^2 = 10.39$, $P = 0.0013$); however, foraging heights were conflated with species observed, as ground foragers (American Robins, Steller's Jays) were more common in developed sites. We observed few species-specific differences in foraging height in developed and undeveloped sites. American Robins foraged higher than 3 m in only two of 60 observations. Only four of 43 Pygmy Nuthatch observations were of birds below 3 m. Mountain Chickadee foraging heights did not differ in low development and high development ($\chi^2 = 0.13$, $P = 0.7198$); neither did those of Steller's Jays ($\chi^2 = 2.71$, $P = 0.0997$), Dark-eyed Juncos ($\chi^2 = 0.06$, $P = 0.8028$), or White-headed Woodpeckers ($\chi^2 = 0.05$, $P = 0.8194$). Steller's Jays tended to forage lower to the ground in high development.

Discussion

Community Structure

The composition of landbird communities in our study changed substantially along the development gradient. Species composition in low, moderate, and high development sites differed significantly, driven by species that were consistently present in low development (e.g., Dusky Flycatcher) or high development (e.g., Brewer's Blackbird) but absent or extremely rare at the other end of the gradient. Removing single species from the MRPP analysis did not substantially affect the significance of the difference in composition among development categories, suggesting that multiple species were driving the overall pattern. Our chief finding from this analysis was the existence of major shifts in composition along the urbanization gradient caused by multiple species being added to or removed from the community. Compositional shifts of this nature in landbird communities have been documented elsewhere.

In our study, landbird communities experienced a steady decline in richness from undeveloped forest to the most urban sites. The prevailing pattern seemed to be one of loss of native species as urbanization increased, rather than the addition of any species at midpoints along the gradient. Species richness of all landbirds was associated most strongly with all factor groups with the exception of landscape-level vegetation. It's not surprising that species richness had a variety of primary influences; as the differences in species composition along the gradient made clear, the landbird community in Tahoe was not uniform in its associations with development, suggesting that multiple abiotic and local habitat features interact with development to affect landbirds. The stand-alone development model was far superior to the other factor groups' models, with development being strongly negatively related to species richness. Another result of the diversity of responses is that the best model only explained about 37% of the variation in species richness.

Importantly, when only the points with human-use data were included in the analysis, human use was the most important factor in explaining species richness. This study is the first to demonstrate that disturbance from human use can be the predominant factor structuring landbird communities. Human use has been shown previously to alter bird communities (Fernández-Juricic 2000) but no research to our knowledge has teased apart development and human use in an urbanization context, where human use is at its highest. Our results suggest that urbanization studies that ignore human use may reach misleading conclusions because population- and community-level effects of human use often mirror those of development (Boyle and Samson 1985; Riffell et al. 1996; Fernández-Juricic 2000). As Miller et al. (2003) noted, such strong effects of human use have profound implications for habitat restoration efforts that recreate suitable vegetation conditions but fail to acknowledge that recreation or other human activities prevent target species and guilds from using restored habitats.

We did not find the peak in richness in moderate development that others (Blair 1996, 2004, Hansen et al. 2005) have found, despite sampling nearly the entire possible range of development values—from 0% to 90% development. In other studies, researchers have found that suburban habitats contain a diverse mix of species because they attract both species that use native habitats and species that use human-dominated habitats. The generality of the peak in richness and abundance at intermediate levels of urbanization is a topic in great need of review or meta-analysis.

Development was not a major factor in overall abundance, but landscape-level vegetation, abiotic factors, and geography were all important. The abiotic model alone was far superior to any other factor group's model; abundance increased with increasing distance to water and decreasing elevation. The increase in abundance with increasing distance to water and decreasing elevation is somewhat surprising, because those two factors are somewhat related in the basin, and birds often congregate near water. Relative abundances of individual species did occasionally peak in moderate development, but wholesale additions of species were nonexistent.

Dominance increased sharply with development, and was most closely related to development and landscape-level vegetation. Examining dominance in conjunction with species richness and abundance was enlightening because it demonstrated that the species lost with increasing development were compensated for (in terms of abundance) by increases in common species, leading to greater dominance. Thus, the urban bird community in the Lake Tahoe basin is a compromised and simplified one, consisting primarily of common, generalist species that are abundant enough to replace the specialists lost from the undeveloped areas.

More definitive relationships were observed with individual functional groups. Surprisingly, ground nesters were associated primarily with landscape and abiotic factors, although all factor groups were somewhat important. We expected local habitat features, development, and human use to be more important for this species group, which we expected to be particularly sensitive to ground disturbance of any kind. The positive association with conifer forest and shrubs within 300 m did show that they were sensitive to loss of natural habitats, however. The species comprising this group—Common Nighthawk, Dark-eyed Junco, Fox Sparrow, Hermit Thrush, Mountain Quail, Nashville Warbler, Savannah Sparrow, Song Sparrow, Spotted Towhee, Townsend's Solitaire, and Wilson's Warbler—all either decreased in abundance with increasing development or had no relationship to development. Retention of native vegetation in surrounding neighborhoods could be vital to maintaining ground nesters in urban forest parcels.

Cavity nesters were associated somewhat with all factor groups, with geography and local habitat features having the strongest influence. Cavity nesters were less abundant on the east side of the basin in the drier, more open forests of the Carson Range. The importance of snags for cavity nesters has long been understood (Raphael and White 1984), and this study's replication of that finding is not surprising. The decline of snags with development and their near absence from urban forests, documented in the vegetation structure component of this study, points to a highly likely impact on cavity nesters in urban areas in the basin. Although several cavity nesters maintain native-forest-like abundance levels in urban areas, they may accomplish this by nesting in buildings, often achieving the status of human conflict species (*sensu* Manley et al. 2000). If additional snags were retained in urban areas, perhaps fewer buildings would have cavities excavated in them and cavity nesters would continue to thrive in the basin's urban areas. The decline in productivity of cavity nesters with development suggests that they are selecting lower quality nest substrates in urban areas, making them more vulnerable to nest failure.

Omnivores have been shown previously to increase with urbanization and the positive association we observed of ground-foraging omnivores with some factors of urbanization—namely, human disturbance and forest clearing—is not surprising. Most of the species comprising this group—the corvids and blackbirds especially—are known syanthropes (Johnston 2001) that have been shown to benefit from human-provided food, thus potentially explaining the increase with human use. The availability of human-provided food typically increases with land clearing for development. Development itself, while being the strongest individual factor-group model by a considerable margin, was not a recurring factor in more complex models—landscape-level vegetation turned out to be more important—again highlighting the importance of considering all factor groups together. This group included some species that are omnivores only in the sense that they typically eat seeds but feed their young insects; were these species omitted we suspect the strong relationships to facets of urbanization we found would have been even stronger.

Finally, invertivorous birds were most associated with abiotic and local habitat factors, although they were somewhat associated with all factor groups. Specifically, areas with moderate slopes, large distances to water, moderate canopy cover, high snag volume, and low tree density yielded greater abundances of invertivores. Canopy cover and amounts of trees and snags are habitat features potentially under management control, and keeping moderate densities of trees and high volumes of snags will go a long way to maximizing invertivore abundance.

In summary, landbird community structure is affected by a variety of factors, including but not limited to urbanization factors. The clear decline in richness with development suggests that urban forests in urbanizing areas may serve an important role in supporting native landbirds. Bird species richness and abundance commonly respond to vegetation composition and structure.

Within urban forests, we found only minor changes in vegetation composition and structure in relation to the surrounding level of development, with the exception of loss of snags and logs. However, in neighborhoods, many more aspects of local vegetation are compromised. Urban forests thus represent relatively intact forests, with the exception of low densities of snags and logs. This illustrates that the management of forest parcels to retain their native composition and natural structural characteristics makes a strong contribution to the maintenance of native landbird species composition in urbanizing environments. Increasing the retention of snags and logs in urban forests is likely to improve their ability to support native landbirds.

Abundance and Productivity

The strong and diverse responses of individual landbird species to development in this study serve to highlight the threat of urbanization to landbird populations in the Lake Tahoe basin. Over one-third of landbirds were significantly less abundant in urban areas, with many species disappearing entirely from the highest end of the development gradient. Several of these species were considered common in the basin that we did not predict to decline. Even some species generally considered synanthropic—that is, commonly cohabiting with humans (Johnston 2001)—such as the American Robin, Steller's Jay, and Brown-headed Cowbird -- tended to decline after the landscape was approximately 50% developed.

High abundance is not necessarily evidence of a healthy population (Van Horne 1983), and studies have shown a disconnection between abundance and reproductive success in disturbed areas (Bock and Jones 2004). Preference by animals for unsuitable habitats is a phenomenon known as an "ecological trap" (Kokko and Sutherland 2001, Battin 2004). That some developed areas have been shown to be ecological traps highlights the importance of data on reproduction.

Nest survival analysis on all species showed that nest success was most different between the two nest strategies we analyzed —cavity and open—with open-nesters having lower success than cavity nesters. Cavity nester success did not appear to decline with development, but open-cup nester success did decline. Greater success of cavity nesters has been shown in other urbanization studies and probably results from lower susceptibility to predation, the cause of most nest failures in our study (unpubl. data). Within the cavity nesters, there was no effect of guild—that is, primary cavity excavators were no more successful than weak cavity excavators or secondary cavity nesters. Within open nesters, ground and shrub nesters fared considerably worse than understory tree nesters, a pattern mimicked in the abundance data. Thus, open-cup nesters associated with substrates at or close to the ground were most impacted as development increased, followed by open-cup nesters selecting higher substrates. Although nest success of the most vulnerable species group appears to be inconsequentially lower - only 2% lower than open-cup nesters associated with higher substrates, and 4% lower than cavity nesters - these differences can easily represent the difference between a sustainable and unsustainable population.

Ecological traps arise when the cues birds use to select habitat for breeding are misleading (Kokko and Sutherland 2001, Battin 2004), resulting in birds selecting habitat that is unsuitable and results in nest failures. One way to look for evidence of ecological traps is by placing birds into one of nine categories based on comparison of abundance-development relationships with nest success-development relationships (Table 2.29). Two species had increasing abundance with development but decreasing nest success: Steller's Jay and Pygmy

Nuthatch. For these two species, nesting in urban forests has the potential to serve to impact the ability of the species to sustain populations in the area -- that is, individuals that nested in urban forests would have nested in elsewhere with greater success. Ultimately, to determine whether urban areas are ecological traps for these species, we would need to know more about population growth rates along the development gradient (Battin 2004).

Table 2.29. Comparison of abundance-development relationship and nest success-development relationship for 10 native landbirds in the Lake Tahoe basin, 2003-2004. Development was measured within 300 m for abundance relationships and either 50, 100, or 300 m for nest success relationships.

		Nest success-development relationship		
		Increasing	Neutral	Decreasing
Abundance-development relationship	Increasing		American Robin	Steller's Jay Pygmy Nuthatch*
	Neutral	White-headed Woodpecker	Mountain Chickadee Northern Flicker	
	Decreasing	Dusky Flycatcher	Western Wood-pewee Red-breasted Nuthatch	Dark-eyed Junco

*Pygmy Nuthatch nest success declined with development in 2003, but not in 2004.

Steller's Jays appeared to partially mitigate the negative effects of living in developed areas by increasingly nesting in buildings, where they were more successful. Buildings likely provide shelter from the elements and protection from predation beyond that provided by trees, jays' primary nest substrate in undeveloped areas. However, a further complication for jays is that rates of destruction or removal of nests in the construction phase appear much higher in buildings (and therefore, in developed areas) than in trees (personal observation), indicating that the total effort a pair of jays puts into a nest may be far greater in developed areas. Vigallon and Marzluff (2005) similarly hypothesized that developed areas (around the Seattle metropolitan area) might be poor-quality habitat for Steller's Jays despite jays' higher abundance there. This species appears to be drawn to urban areas, perhaps by human-provided food—for example, they are a common feeder bird in Tahoe—but increased predation and interference by people keeps them from being highly successful. However, Steller's Jays are known nest predators, and whether they are reproductively successful or not, increased populations of jays in urban areas might account for some of the reduced populations and low nest success of other species.

Pygmy Nuthatches increased in abundance with development, perhaps because of their ability to nest in multiple substrate types, including buildings. Their nest success declined to near zero in the most developed areas in 2003, while holding constant at 100% in 2004, suggesting that food resources, which are more likely to vary year to year than other factors, might have played a role in lowered nest success.

The contrast among the basin's three nuthatch species is especially intriguing. White-breasted Nuthatches had a similar plasticity of nest-site selection to that of Pygmy Nuthatches, but decreased in abundance with increasing development. Nest success data on White-breasted Nuthatches were insufficient for us to perform nest survival analysis. Red-breasted Nuthatch abundance decreased substantially with increasing development. The species was uniformly successful in both developed and undeveloped areas, although most nests were located at the low end of the development gradient. They nested exclusively in snags, which the forest structure component of the study demonstrated are lacking in the basin's urban forests. In addition, Red-breasted Nuthatches did not visit bird feeders established in another component of this study (unpubl. data), while the other two species did, suggesting that Red-breasted Nuthatches might have a fear of novelty that prevents them from nesting in or foraging on human structures. Other species such as chickadees, robins, and jays, seem to lack the neophobic tendency to avoid novel nest sites and are able to successfully reproduce in urban areas more readily. In the case of jays, we have shown an increase in nest success when nests are in buildings. The ability of certain species, and certain individuals within species, to succeed in novel environments is a recent focus in animal behavior (Greenberg 1989, Lefebvre et al. 2001, Dingemanse et al. 2002, 2004 Sol et al. 2002) that holds promise for addressing ecological and conservation questions. Behavioral research on Tahoe's birds could yield substantial insights into the patterns presented here.

Dark-eyed Juncos held the distinction of being the only species in our study to decrease in both abundance and nest success with increasing development. This result was not particularly surprising, as we predicted that birds that nest on the ground and birds that forage on the ground could be highly susceptible to impacts from development, and juncos do both. Although they are one of the most abundant birds in the basin (Roth et al. 2004) they seem highly affected by Tahoe's urban development. Further, for juncos, some years appeared to be worse than others; in 2004 nest success was near zero in high development. Whether urban populations can be replenished after poor breeding years is a topic for further study. Further work is also needed to determine whether reduced abundance and nest success are a result of habitat features, human use, or simply loss of habitat.

Dusky Flycatchers are another interesting case. Their decrease in abundance with increasing development was the strongest we found, and they were not found nesting in sites with >6% development. Nonetheless, their nest success increased with slight increases development. Given their absence at higher levels of disturbance, they are clearly vulnerable to various factors associated with development that are most likely associated with disturbance as opposed to changes in vegetation, which were minimal across our study sites.

Habitat use

We expected that birds would nest and forage higher off the ground in areas of high development and high human use. Nest heights of most species and species groups did not change in the face of greater development or human use, with exception of primary cavity excavators. The lower nesting of primary cavity excavators with increasing development could be a function of decreasing substrate heights.

We also expected that cavity nesters would use substrates in proportion to their occurrence, meaning that they would nest in live or alternative substrates more often than snags in more developed sites, where dead substrates (snags and logs) are less common. We did not see strong patterns across all cavity nesters. However, Mountain Chickadees, as well as the guild to which they belong, weak cavity excavators and secondary cavity nesters, tended to use more live substrates in high development. From this result we can tentatively conclude that live substrates are suboptimal for these species and that they select them for nests only when fewer dead substrates are available, as is the case in more developed areas. Thus, the retention of snags in urban forest would make a contribution to supporting cavity nesters, even snags that are lower heights.

Western Wood-pewee nest success declined with decreasing nest heights, which were lower in lower development, suggesting that pewees were forced to nest lower to the ground in developed areas than would be optimal. There was no direct relationship between nest success and development, however. Thus, the retention of native understory vegetation at levels typical of native forests would help avoid this impact.

Chapter 3:

Small Mammals

Introduction

Squirrels and chipmunks play an important role in forest ecosystem dynamics. Chipmunks and squirrels serve as the primary prey base for forest carnivores, including weasels (*Mustela spp.*), marten (*Martes americana*), coyote (*Canis latrans*), and bobcat (*Felis rufus*) (Bartels and Thompson 1993, Steele 1999). Raptors, such as owls and Accipiters, are also known to prey upon Sciurids (Gordon 1943, Carey 1995). In turn, squirrels prey upon the nests of forest dwelling birds (Adams 1939, Warren 1942, Tevis 1953), in addition to chipmunks (*Tamias* sp.) (Cameron 1967) and lizards (Tevis 1953).

Sciurids also act as important dispersal agents for tree and shrub species and thereby affect forest regeneration and stand structure. For example, Douglas squirrels (*Tamiasciurus douglasii*) have been shown to have a tight association with both cone crop abundance and particular species of cone-bearing conifers, such as fir (*Pseudotsuga*, *Abies*), spruce (*Picea*), and hemlock (*Tsuga*) (Steele 1999).

In addition to predation and food availability, habitat suitability may be an important factor in determining the distribution and abundance of particular Sciurid species. Habitat features such as fallen logs, stumps, snags, rocks, and litter may provide necessary cover for many of the chipmunk and squirrel species (Sumner and Dixon 1953, Clawson et al. 1984, Bartels and Thompson 1993). Some species, such as long-eared chipmunk (*Tamias quadrimaculatus*) and shadow chipmunk (*Tamias senex)*, can tolerate denser forest conditions (Stephens 1906, Sharples 1983), while other species, such as yellow-pine chipmunk (*Tamias amoenus*), lodgepole chipmunk (*Tamias speciosus*), and golden-mantled ground squirrel (*Spermophilus lateralis*), require more open conditions as long as suitable cover is available (Sutton 1992, Bartels and Thompson 1993). Understory and tree density are likely to be impacted by the history of land use in an intensively modified landscape such as the Lake Tahoe basin. Competition among sympatric chipmunks and squirrels may also affect abundance patterns of these species (Carey 1995).

Methods

Sherman Live Trapping

From 2003-2005, 71 different sites were sampled, and 26 of these sites, representing the range of development conditions on the north and south shores of the lake, were sampled in all years. Small mammal populations were sampled using live-traps. Trapping grids of 64 traps (8 x 8) were established at each site, with 15m spacing between stations. Each grid covered ~ 1.1 ha and included a combination of 43 extra-long (3 x 3.75 x 12”) and 21 large (4 x 4.5 x 15”) Sherman live-traps (Fig. 3.1). Traps were run for four consecutive days (= 8 sampling occasions). Traps were set and opened before noon on the first day, then checked twice a day (morning before 10 am and late afternoon before 8pm) through the morning on the last day, after which they were removed. Each trap station was uniquely numbered with a fluorescent orange clothes pin placed in a visible location near the trap to aid in relocation. Traps were baited with a mixture of rolled oats, millet and sunflower seeds and covered with sufficient plant matter (pine needles, bark, sticks) to provide insulation and protect captured animals from the elements. Polystyrene batting was placed in every trap to provide warmth when overnight temperatures were below 40^{O}F.

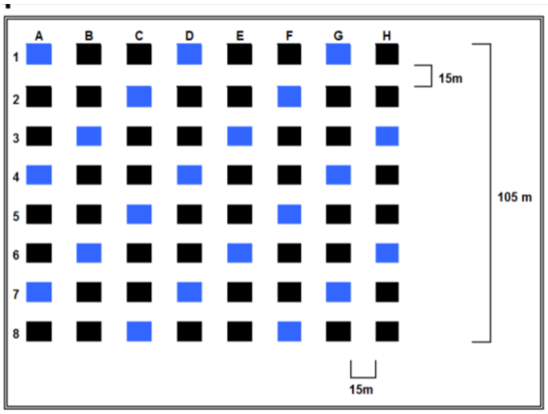


Figure 3.1. Schematic of the trapping grid configuration. Black squares represent extra-large Sherman traps, and blue squares represent large Sherman traps.

Captured individuals were processed and released, and fresh bait was added to traps as needed. All individuals captured were identified to species and data on sex, age (juvenile or adult), weight, reproductive status (males: testes enlarged; females: vagina perforate, nipples swollen, enlarged, reddened, lactating, pregnant) and capture status (new capture or recapture) were recorded. Standard morphological measurements were taken from individuals with questionable species identity. In addition, the closest notable landscape feature (i.e. tree, log, shrub, rock, bare ground) was noted for each capture event. Disturbed, closed or non-functional traps were also recorded at each site visit.

Data Analysis

Community Structure

The effect of a variety of explanatory factors (Table 3.1) on species richness, total relative abundance, and the relative abundance of four functional groups (Table 3.2) were explored with multiple regression analyses. Relative abundance measures were computed from initial captures and scaled for sampling effort. Functional groups were selected based on common habitat and dietary requirements, since animals in these groups may respond similarly as a group to urbanization depending on the direct and indirect impacts of development and human disturbance. Functional groups include arboreal squirrels, terrestrial granivores, terrestrial herbivores, and insectivores. Deer mice (*Peromyscus maniculatus*) were not included in the relative abundance estimates, because they were not handled in all sampling years. However, presence of deer mice were noted at all sites in all years; therefore, they were included in estimates of species richness.

First, a multiple regression model was generated for each small mammal response variable with explanatory variables grouped by habitat (abiotic, ground vegetation, canopy vegetation, CWHR habitats and habitat types), development, disturbance and predator factor groups (Table 3.1). Each explanatory factor group model then represented different hypotheses regarding what is driving the response variables (i.e., habitat vs. abiotic factors vs. development vs. disturbance vs. predators). Covariates of year, sampling date, and spatial location were also included in the models. Data for each explanatory factor was standardized for analysis so that the relative value of the model parameter estimates could be comparable in terms of relative parameter influence. We checked the data for outliers and nonlinear relationship by visually examining the scatter plots of each response variable against each explanatory factor. For two of the functional groups, terrestrial granivores and herbivores, the relationship between percent developed are within 300m and relative abundance appeared to have a unimodal distribution. Therefore, the potential of a quadratic relationship between these variables was explored by using the quadratic form of development at 300m as an explanatory factor in the models for the total abundance of these functional groups. In the case of habitat types, broader habitat classifications (i.e., coniferous forest, shrubland) were included in models of species richness and total relative abundance models, since species within these groupings are expected to have different specific habitat requirements. On the other hand, models of functional groups included more specific habitat types based on California Wildlife Habitat Relationship (CWHR) habitats, because species within these groups are more likely to share specific habitat requirements. In all cases, overall habitat heterogeneity, that is number of different habitat types, was also used as a factor in the habitat types explanatory group models.

Competing hypotheses were compared using Akaike's Information Criterion (AIC_C) model selection procedure to determine the best explanatory models for each response variable (Burnham and Anderson 2002). First, full factor group models were compared to determine the best global model for each response variable. The full model for each explanatory factor group was then reduced to a model that included only those factors that resulted in the best-fit model for each response variable based on AIC_C model selection. For each factor group, each variable was removed one by one with replacement; those variables that, in their absence, resulted in a higher AIC_c, were included in the best-fit model. The reduced models for each explanatory factor group were then compared to one another with AIC_C model selection to determine the factor groups that had the greatest influence on each small mammal response variable.

Finally, single best-fit model was generated for each small mammal response variable. Each best-fit model included a combination of factors from the reduced explanatory group models. For explanatory groups that were compared at multiple spatial scales (i.e., habitat type at 100m, 300m, and 500m; development at 100m, 300m, and 1000m), only factors from the scale with the highest model rank in the reduced model comparison was used in the subset models due to a high degree of correlation among these factors at the different scales. Best-fit models were determined by fitting a full factor group model and removing each variable with replacement until only those factors that lowered AIC_C model remained. The highest ranked models for each response variable are summarized.

The effect of development on species composition was examined using multi-response permutation procedure (MRRP). All sites were categorized by development values (no = 0-1%, low = 1-30%, and high > 30% developed within 300m of the site center point), and presence-absence data for all sites was used to test for differences among the groups using similarity based on Sørenson's distance values (McCune and Grace 2002). A natural weighting factor ($n/\Sigma [n]$) was applied to the samples, and significance was based on the distribution of 1000 permutations of group associations (McCune and Mefford 1999). In order to assess the relative impact of each species on species composition, each species was removed individually with replacement. The greater the change in the test statistic, the greater the contribution of a species to observed differences in overall species composition.

Table 3.1. Explanatory factors and covariates used in multiple linear regression analyses evaluating the relative impact of habitat, development, disturbance and predators on species richness and abundance.

Explanatory Variables	**Factors**
Covariates	• Year • Julian date of sampling • Spatial location (UTM coordinate X multiplied by coordinate Y)
Habitat	**Abiotic** • Elevation • Slope • Precipitation **Ground vegetation** • % cover of: shrubs, herbs, grasses, bare ground, litter, rock • Coarse woody debris (CWD), total estimated volume **Canopy vegetation** • % cover of trees • Total number of trees, 3 size classes: 12-27mm, 28-60mm, >60mm • Snags, total estimated volume **CWHR habitat * (used in functional group abundance models)** • % cover of each habitat type, 3 scales: 100m, 300m, 500m • Habitat heterogeneity (total number of different habitat types), 3 scales: 100m, 300m, 500m • CWHR habitat types found in the Lake Tahoe basin include: ASP, BAR, JPN, LAC, LPN, MCP, MRI, PGS, RFR, SCN, SGB, SMC, URB, WFR, WTM **Habitat types (used in species richness and total abundance models)** • Based on groupings from CWHR habitat types: Coniferous forest, Shrubland, Grasses, Aspen, Meadow-Riparian, Bare ground • % cover of each habitat type, 3 scales: 100m, 300m, 500m • Habitat heterogeneity (total number of different CWHR habitat types), 3 scales: 100m, 300m, 500m
Development	• % development from site center at 3 scales: 100m, 300m, 1000m radius
Disturbance	• People per hour • Dogs per hour
Predators	• Domestic dogs • Domestic cats • Native species richness

Table 3.2. Summary of response variables used in the multiple regression analyses.

Response Variables	**Description**
Species Richness	- Total number of small mammal species captured at each site
Total Relative Abundance	- Abundance of all small mammals based on initial captures and scaled for sampling effort
Functional Group Relative Abundance	**Arboreal squirrels** - Douglas squirrels, northern flying squirrels, gray squirrels **Terrestrial granivores** - Chipmunks, ground squirrels **Terrestrial herbivores** - Voles, western jumping mice **Terrestrial insectivores** - Shrews

Population Dynamics

The three consecutive years of mark-recapture data from 26 sites on the north and south shore of the Lake Tahoe basin was used to test a set of specific a priori hypotheses regarding the influence of age, sex, time, urban development and human-associated disturbance on chipmunk, ground squirrel and Douglas squirrel populations. This sampling design fits the criteria for a robust design (Pollock 1982), where trapping episodes are distinguished by both primary and secondary sampling intervals. Primary sampling occurred each year (2003, 2004 and 2005), representing intervals over which population gains or losses are expected. Secondary sampling periods consisted of the four consecutive days (8 trap occasions) that traps were operating at each site. During this interval the population is assumed to be closed to gains and losses (Kendall et al 1997). The robust design can account for temporary emigration from study sites and improves estimates of population size by relaxing the assumption of a closed population between primary sampling periods. The data generated by the robust design can then be analyzed with appropriate population models that provide estimates of demographic parameters (Seber 1982, Pollock 1982, Kendall et al. 1995), including survival, emigration rate and abundance (Kendall et al. 1997).

Program MARK (White and Burnham 1999) was used to generate models to estimate survival, emigration, capture probability and abundance in each species under various parameterization structures. Data for the primary periods were analyzed using open population models, while the secondary samples were analyzed using closed population models that allow for unequal capture probability (Otis et al. 1978, White et al. 1982). An information-theoretic approach to model selection was used to assess multiple hypotheses using AICc (Akaike's information criterion adjusted for small sample bias; Burnham and Anderson 1998) values and relative model weights to select the hypotheses that best fit the data for each species (Burnham and Anderson 1998, Anderson et al. 2000). We first tested hypotheses concerning the effect of group (assigned by age {adult vs. juvenile} and sex {male vs. female}) and time (year or capture occasion) on survival, emigration, capture probability and abundance. Once this set of models was generated, the highest-ranking model based on AICc weight was used to test for the effect of covariates related to urban development and disturbance on survival and emigration. These covariates included percent of developed land area at multiple spatial scales (100m, 300m, 500m, and 1000m), frequency of human use at the site, and frequency of dog use at the site. Model selection was again performed in a sequential manner until a set of models that best fit the data were generated.

From the highest ranked models, we explored the functional relationship between development or disturbance and survival or emigration, by producing parameter values at specified levels of the covariate. The resulting parameter values were then plotted against the covariate to illustrate the relationship between the two.

In order to generate parameter estimates as a function of a particular covariate, the beta values from a model were back-transformed. Since the logit link function was used to transform the data in the models, the back-transformation formula used was:

$$\text{logit}(\phi) = \frac{e^{(\beta0 + \beta1*X1 + \beta2*X2)}}{1 + e^{(\beta0 + \beta1*X1 + \beta2*X2)}}$$

Where ϕ is the parameter of interest (i.e. survival), β_0 is the beta estimate for the intercept, β_1 is the beta estimate for a particular parameter (i.e. adult males or time), and β_2 is the beta estimate for the covariate. The X values correspond to the respective standardized values of a parameter, generated by subtracting the mean and dividing by the standard deviation:

$$X(n) = \frac{m_n - M}{SD_M}$$

Where m_n = particular value of a parameter, M = mean value of parameter, and SD_M = standard deviation of parameter. So at the mean value of a parameter, $X(n) = 0$, and at one standard deviation from the mean $X(n) = -1$ or 1.

Results

Community Structure

From 2003-2005, over 31,000 trap nights resulted in the capture of 6,400 individuals and 19 species (Table 3.2). Total species richness averaged 5.3 species per site (range = 2 to 9), and species richness for squirrels and chipmunks was 4 species per site on average. The average number of small mammals captured per 100 trap nights per site, excluding deer mouse, ranged from 3.2 to 54.9 individuals (mean = 19.7, s.d. = 10.98). On average of over 95% of these individuals were squirrels and chipmunks (mean = 19.1 individuals per site, s.d. = 11.12). Figures 3.2 and 3.3 show small mammal species richness and total relative abundance along the 300m development gradient.

Table 3.2. Small mammal species captured from 2003 to 2005.

Scientific name	**Common name**	**Code**
Rodentia		
Sciuridae		
Glaucomys sabrinus	Northern flying squirrel	GLSA
Sciurus griseus	Western gray squirrel	SCGR
Spermophilus beecheyi	California ground squirrel	SCGR
Spermophilus lateralis	Golden-mantled ground squirrel	SPLA
Tamias amoenus	Yellow-pine chipmunk	TAAM
Tamias quadrimaculatus	Long-eared chipmunk	TAQU
Tamias senex	Shadow chipmunk	TASE
Tamias speciosus	Lodgepole chipmunk	TASP
Tamiasciurus douglasii	Douglas squirrel	TADO
Muridae		
Microtus longicaudus	Long-tailed vole	MILO
Microtus montanus	Montane vole	MIMO
Neotoma cinerea	Bushy-tailed woodrat	NECI
Peromyscus maniculatus	Deer mouse	PEMA
Peromyscus truei	Pinon mouse	PETR
Zapodidae		
Zapus princeps	Western jumping mouse	ZAPR
Insectivora		
Soricidae		
Sorex trowbridgii	Trowbridge’s shrew	SOTR
Sorex vagrans	Vagrant shrew	SOVA
Lagomorpha		
Leporidae		
Lepus americanus	Snowshoe hare	LEAM
Sylvilagus nutallii	Mountain cottontail	SYNU

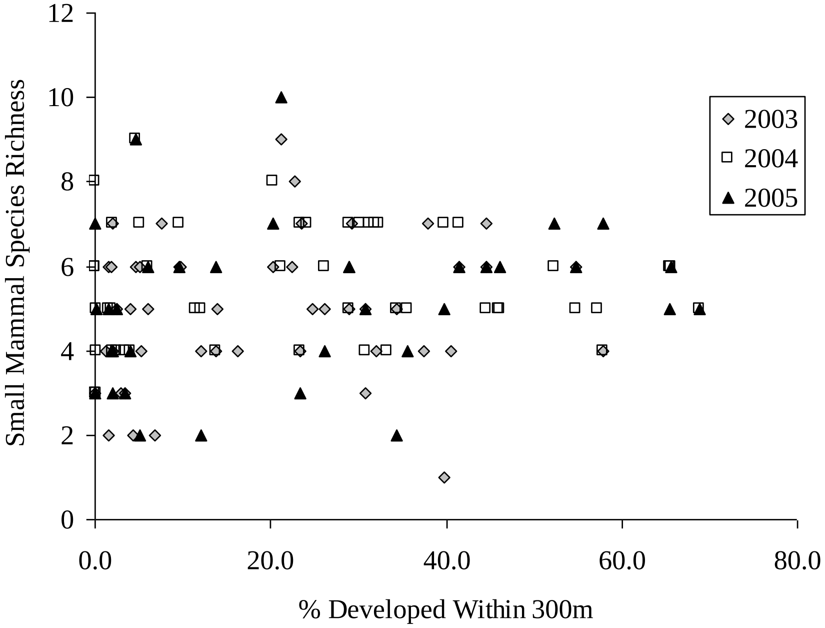


Figure 3.2. Small mammal species richness as a function of percent developed area within 300m of each sampling location.

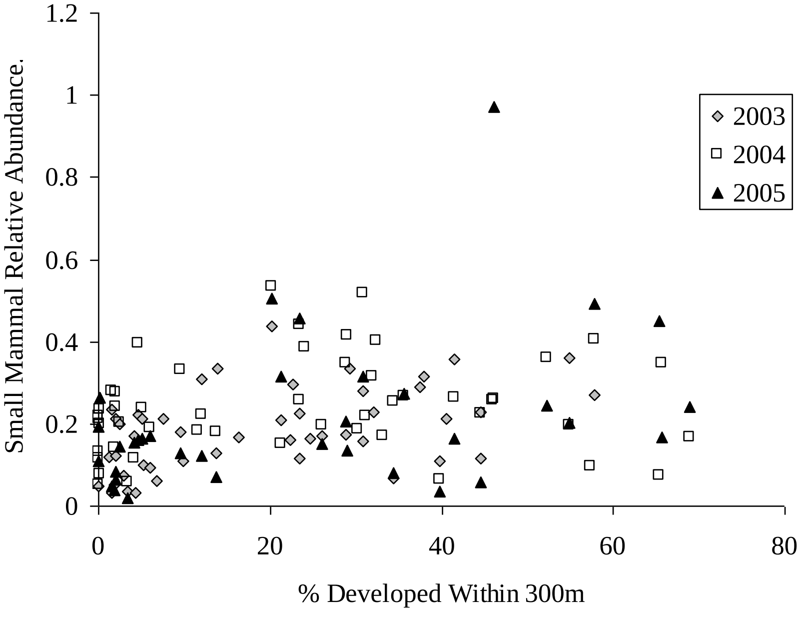


Figure 3.3. Small mammal relative abundance as a function of percent developed area within 300m of each sampling location.

Community composition was significantly influenced by development as assessed by the MRPP analysis (T = -4.409, p < 0.001; Table 3.3). Sites with no development (0-1%) did not differ significantly from low or high development sites (T = -1.233, p = 0.114 and T = -1.366, p = 0.097, respectively), there was a significant difference in species composition between low and high development sites (T = -5.586, p < 0.001). These results indicate that the greatest difference contributing to the overall difference in composition among development classes is attributable to the comparison of low and high development groups. MRPP results indicate that no one species was responsible for the differences we observed among development groups, indicated by the fact that development groups were still significant regardless of which species was removed (Table 3.3). Rather, that it was a combination of responses individual species that created differences in composition among development levels.

Table 3.3. Results of the Multi-Response Permutation Procedure (MRPP) analysis on small mammal species composition at 72 sites grouped by development class: 0-1%, 1-30%, or >30% developed. **T** is a test statistic that measures the degree of difference in species composition among these 3 development categories. The change in **T** (**ΔT**) indicates the relative influence the removal of a single species has on the observed difference in species composition. Positive values are associated with species that decrease the overall difference in species composition, and negative values are associated with species that decrease overall similarity.

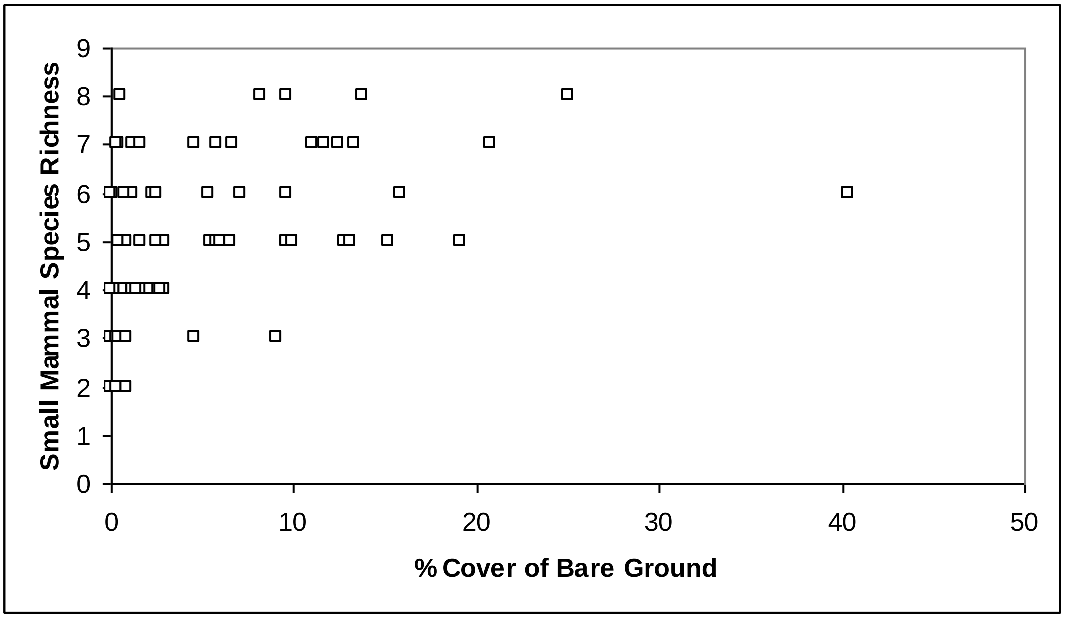
Species removed	**T**	**ΔT**	***P***
None (all species present)	-4.409		< 0.001
Contribute to diversity:			
Voles	-2.602	1.807	0.015
Golden-mantled ground squirrel	-3.114	1.295	0.028
Deer mouse	-3.263	1.146	0.004
Long-eared chipmunk	-4.289	0.120	0.039
Lodgepole chipmunk	-4.361	0.048	<0.001
Contribute to homogeneity:			
Shrews	-4.448	-0.039	<0.001
Northern flying squirrel	-4.494	-0.085	<0.001
Western gray squirrel	-4.561	-0.152	0.042
Douglas squirrel	-4.716	-0.307	<0.001
Shadow chipmunk	-4.771	-0.362	0.043
California ground squirrel	-4.955	-0.546	0.046
Yellow-pine chipmunk	-5.011	-0.602	<0.001

Multiple regression analysis and the model selection procedure identified important factors that influence small mammal species richness and relative abundance in the Lake Tahoe basin. While development at all spatial scales (100m, 300m, and 1000m) and disturbance at the site were important predictors of small mammal species richness in the full regression models (Appendix 3.1), explanatory factors including percent cover of bare ground, sampling year, habitat heterogeneity at the 300m scale, Julian sampling date were identified as the most influential factors in the reduced models (Appendix 3.2). Models including these factors accounted for over 75% of the model weights. These factors, with the exception of Julian sampling date, were also in the best-fit model, which is a subset of factors yielding the lowest AIC_C score relative to other combinations subset models (Table 3.4).

Percent cover of particular understory features, including herbs, rocks, litter and CWD, as well as the amount of any single habitat type (coniferous forest, shrubland, grassland or aspen forest) were negatively associated with species richness. Habitat heterogeneity at the site and in the area immediately surrounding a site positively affected small mammal species richness. That is, the number of different CWHR habitat types within 300m of a site positively affected the number of species observed. In addition, the percent cover of bare ground also positively affected small mammal species richness. Other potentially important associations with species richness identified by reduced models with weights greater than 5% were positive relationships with percent-developed area at the 1000m scale, frequency of human use per hour, habitat heterogeneity at the 100m scale, and the presence of domestic dogs (Appendix 3.2). Sampling year was also an important determinant of overall species richness, with more species being detected per site in 2004 than in 2003 or in 2005.

We looked at the relationship between bare ground and species richness in more detail (Fig. 3.4a) and not surprisingly we found a significant univariate relationship ($R^2 = 0.16$, Adj-$R^2 = 0.15$, $p = 0.0006$). More importantly, we found that as bare ground ranged from 0 to 25 %, the minimum number of species detected increased from 2 to 5 species, indicating that the presence of bare ground was a limiting factor for a few species. This relationship breaks down when yellow pine chipmunk and golden-mantled ground squirrels are removed ($R^2 = 0.05$, Adj-$R^2 = 0.04$, $P = 0.0596$). Therefore, it is likely the affinity of these two species for bare ground that is driving the relationship between small mammal species richness and bare ground. Further, only one site exceeded 25% bare ground, so the strong associations between richness and bare ground that we observed reflect conditions where bare ground is not frequently occurring or abundant where it occurs. The amount of bare ground was not reflect human-caused ground disturbance ($R^2 = 0.02$, Adj-$R^2 = 0.01$, $P = 0.188$; Fig. 3.4b), as one might suspect, but rather a function of natural factors (e.g., slope, vegetation density, site moisture). The relationship between bare ground and litter is much stronger ($R^2 = 0.30$, Adj-$R^2 = 0.29$, $p < 0.001$) than with human disturbance.

a) species richness relative to bare ground



b) bare ground relative to localized development

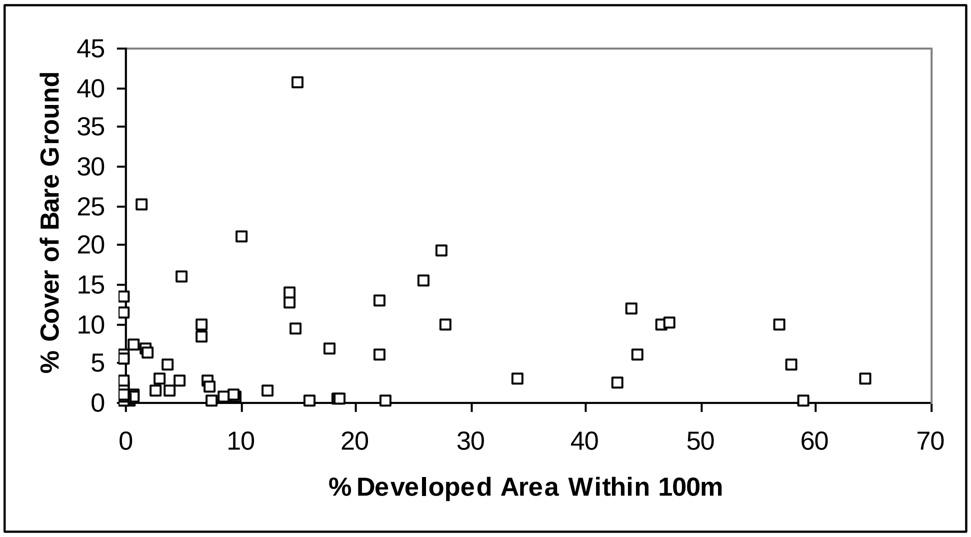


Figure 3.4. The relationship between (a) small mammal species richness and percent bare ground, and (b) bare ground and percent development within 100 m at 71 sites sampled in the Lake Tahoe basin in 2003-2005.

The total relative abundance of small mammals was best explained by ground vegetation features in both the full and reduced models (Appendix 3.3 and 3.4). Characteristics of the ground vegetation were identified as the most important factors affecting relative abundance, with a model weight of 99% for this explanatory factor group. Specifically, the percent cover of bare ground was positively associated with abundance, as it was for richness, while the percent cover of herbs, rock, litter, and total volume of coarse woody debris had negative associations with abundance (Appendix 3.3 and 3.4). However, when the best factors from the reduced models were run together, only the percent cover of herbs and bare ground remained in the best-fit model total abundance (Table 3.4). In addition, the best-fit model estimated negative relationships between total relative abundance and frequency of human use at the site, as well as the amount of coniferous forest, shrubland, grassland, and aspen habitat at the 500m scale. In contrast, percent-developed area at the 300m scale was positively associated with abundance (Table 3.4).

The univariate relationship between total abundance and bare ground was remarkably strong and consistent ($R^2 = 0.42$, Adj-$R^2 = 0.41$, $P < 0.001$); maximum and minimum abundance increased with the cover of bare ground (Fig. 3.5). Again, this relationship breaks down when yellow pine chipmunk and golden-mantled ground squirrel abundance are removed ($R^2 = 0.006$, Adj-$R^2 = -0.009$, $p = 0.538$). Therefore, it is likely the affinity of these two species for bare ground that is driving the relationship between small mammal relative abundance and bare ground.

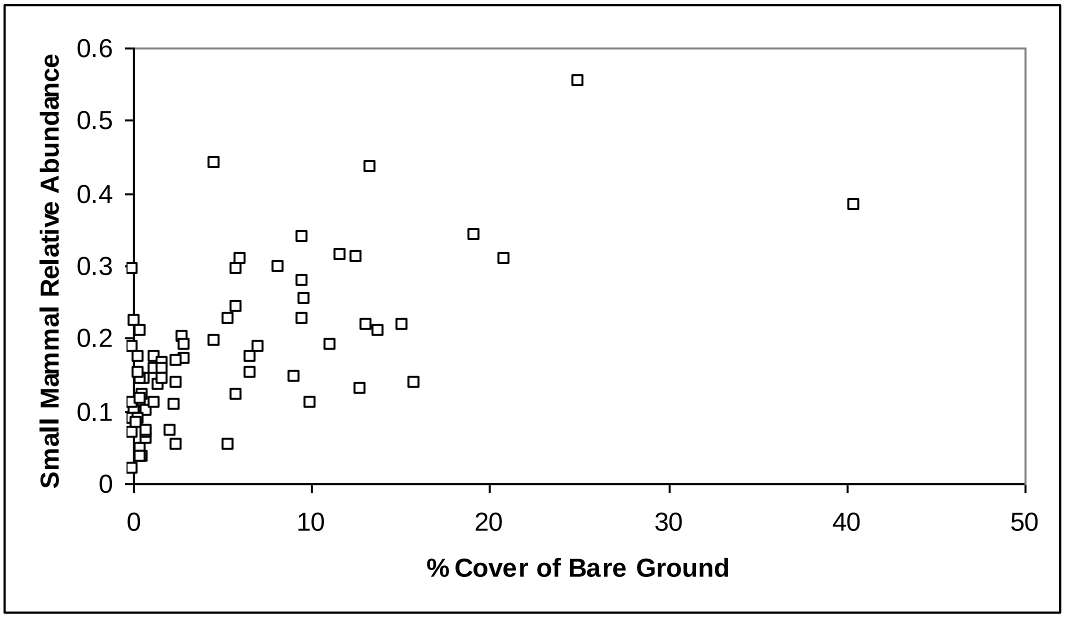


Figure 3.5. The relative abundance of small mammal species as a function of the percent cover of bare ground.

We also looked at patterns of frequency of occurrence and dominance in among species along the development gradient (Fig. 3.6 and 3.7, respectively). Three species were consistently more frequently occurring at sites with higher surrounding development: Douglas squirrel, yellow pine chipmunk, and voles. Long-eared chipmunk, shadow chipmunk, northern flying squirrel, and deer mouse were consistently less frequently occurring with higher surrounding development. Seven species were numerically dominant at one or more sites (Fig. 3.7). Yellow pine chipmunk was frequently the dominant species, and it was more frequently dominant at higher development. Long-eared chipmunk was the second most frequently dominant species, but it was dominant less often at higher development sites, suggesting that development shifts the competitive advantage from long-eared to yellow pine chipmunks. Shadow chipmunk also loses dominance at higher development levels. Although California ground squirrel was not often numerically dominant, it appeared to increase in abundance and frequency of dominance at higher development.

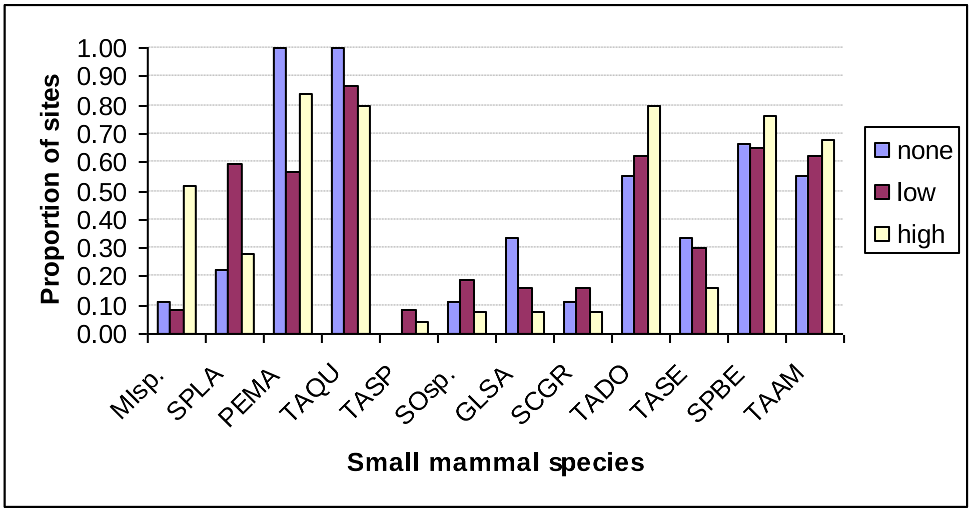


Figure 3.6. Proportion of sites occupied by each small mammal species observed by development within 300 m (none = 0% developed, low = 0-30% developed, high > 30% developed).

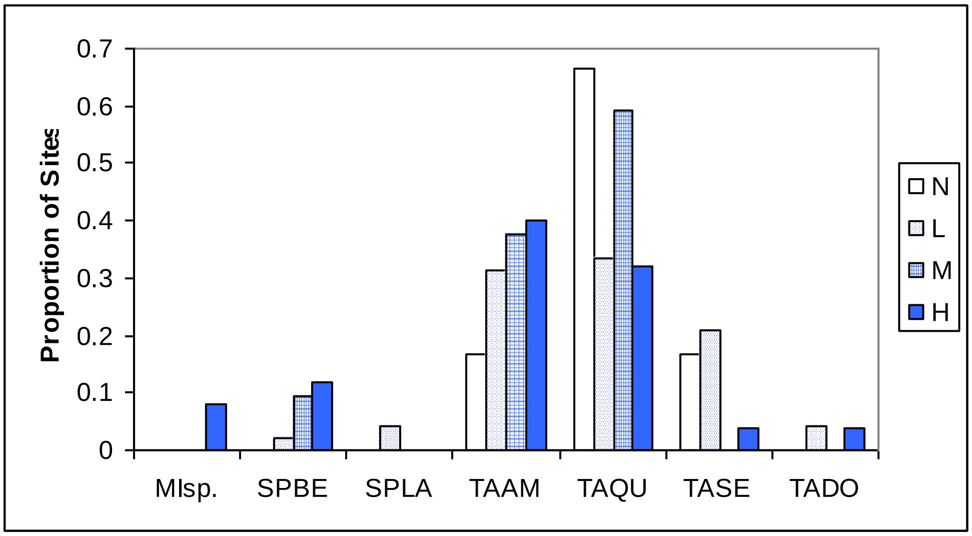


Figure 3.7. Proportion of sites in each of four development classes at which each individual small mammal species were numerically dominant. Development (within 300 m) classes: N = 0%; 0% < L < 15%; 15% < M < 30%; H > 30%. Samples sizes for development classes were 6, 24, 16, and 25 sites, respectively.

Functional Groups

Small mammal functional groups displayed unique responses to the various environmental factors that we explored. For arboreal squirrels (a group dominated by Douglas squirrels), development at the 1000m scale was the best full model of abundance (Appendix 3.5), but habitat heterogeneity at the site scale (100m) and the presence of domestic dogs were included in the best reduced models of abundance (Appendix 3.6). These factors were both positively associated with tree squirrel abundance. The other two models with weights greater than 5% showed squirrel abundance to have a positive relationship with percent-developed area at the 1000m scale and a negative relationship with the percent cover of rock at the site (Appendix 3.6). The association with habitat heterogeneity and the percent cover of rock at the site were the only factors that remained in the best-fit model of arboreal squirrel abundance (Table 3.4).

For terrestrial granivores (ground squirrels and chipmunks), ground vegetation characteristics were the most influential factors affecting relative abundance in the best full, reduced, and best-fit models (Appendix 3.7, 3.8, and Table 3.4). The reduced and combined models revealed that the factors percent cover of herbs and bare ground are particularly influential on relative abundance (Appendix 3.7, 3.8). While percent cover of herbs was negatively associated with abundance, there was a positive association with the percent cover of bare ground. In the best-fit models, a positive relationship between terrestrial granivore abundance and percent-developed area at the 300m-scale was revealed, in addition to a negative relationship with native predator species richness (Table 3.4).

For terrestrial herbivores (a group composed primarily of long-tailed voles with some observation of jumping mice), there was concordance among the single best full, reduced and combined factor model that the quadratic effect of development at the 300m scale was the single most important factor positively affecting relative abundance (Appendix 3.10, 3.11 and Table 3.4).

Finally, the best full explanatory factors group models for insectivore (shrew) relative abundance were models of predator presence and disturbance at the site (Appendix 3.11). However, the best reduced models showed that combination of the percent cover of Sierran mixed conifer and white fir habitat type at all three spatial scales (100m, 300m and 500m) was an important factor positively influencing insectivore relative abundance (Appendix 3.12). In addition, the percent cover of montane riparian habitat and the combination of red fir and subalpine conifer habitat at the 100m scale were also important positive factors in the highest ranked model (Appendix 3.12). In the best-fit model, the amount of montane riparian and Sierran mixed conifer - white fir habitat at the 100m scale are the most important factors positively related to insectivore abundance (Table 3.4).

Table 3.4. Best-fit models for each small mammal response variable. Models that included a subset of factors from the top-ranked reduced model for each explanatory factor group were compared based on AIC_C scores and model weights to identify the combination of explanatory factors that best fit each response variable. Presented here are the equations for the best-fit models, as well as R^2, adjusted R^2 (Adj-R^2), and the model p-value.

Response Variable	**Best fit model equation**	**R^2 (%)**	**Adj - R^2 (%)**	**p-value**
Species richness	4.85 + 0.763_*Year03-04* + 0.349_*Habitat heterogeneity 300m* + 0.469_*% Bare ground*	23.76	20.35	0.0004
Relative abundance	0.179 – 0.19_*Aspen 500m* – 0.067_*Coniferous forest 500m* – 0.025_*Grassland 500m* – 0.030_*Shrubland 500m* – 0.033_*% Herbs* + 0.058_*% Bare ground* + 0.023_*Development 300m* – 0.017_*People/hr*	68.81	64.78	<0.0001
Arboreal squirrel abundance	0.013 + 0.006_*Habitat heterogeneity 100m* – 0.004_*% Rock*	19.23	16.85	0.0007
Terrestrial granivore abundance	0.156 + 0.031_*Development 300m* – 0.037_*% Herbs* + 0.057_*% Bare ground* – 0.014_*Native predator species richness*	59.62	57.17	<0.0001
Terrestrial herbivore abundance	0.008 + 0.006_*Development 300m* + 0.007_(*Development 300m*^{2})	39.71	37.93	<0.0001
Insectivore abundance	0.0009 + 0.0006_*Montane riparian 100m* + 0.0007_*Sierran mixed conifer/White fir 100m*	18.60	16.21	0.0009

Population Dynamics

The response of individual species to environmental factors is the key to understanding what shapes small mammal communities in the basin, and population responses are critical to identifying tolerances and thresholds of individual species that are most sensitive and may be at risk.

Due to the small sample size relative to the number of population parameters of interest, we first reduced overall model complexity in order to generate reliable parameter estimates for the hypotheses tested. First, we reduced the parameter index matrices (PIMs) by setting recapture probability equal to capture probability (P) and immigration rate equal to emigration rate (G), so there were only parameter estimates generated for initial capture probability and emigration-immigration. For three species of chipmunk -- yellow-pine, shadow and lodgepole chipmunk -- and Douglas squirrel, the recapture rate between years was too low to generate reliable emigration-immigration parameters, so this parameter was fixed at zero for models of these species. For the two species observed at the fewest number of sites -- shadow and lodgepole chipmunk -- it was not possible to produce reliable population estimates even with the “dot” model. However, models for these species were able to generate estimates of survival and capture probability.

We report on the 10 top-ranked models for each species, in addition to graphs depicting the functional relationship between survival or emigration and pertinent covariates relating to development and disturbance. All the detailed output from population modeling is provided in Appendices 3.13 to 3.19. .Model averaging was used to generate real parameter estimates, and estimates of abundance are presented graphically as a function of sampling year.

Long-eared chipmunks were the most numerous and evenly distributed of all the small mammal species sampled. Model selection revealed that sampling year was the most important determinant of survival rate (Table 3.5), with annual survival being greater between 2003 and 2004 ($S = 0.4002$, $SD_S = 0.0348$) than between 2004 and 2005 ($S = 0.1415$, $SD_S = 0.0207$) (Fig. 3.8). Development at the 1000m spatial scale also influenced survival (Table 3.5; Fig. 3.8), but the decrease in survival with increasing development was less pronounced than the year effect. Emigration-immigration was most affected by group affiliation, as well as development at the 1000m scale (Table 3.5; Fig. 3.9), with emigration-immigration rates increasing with development. Juvenile males and females were more likely to move into and out of a site than adult males (Fig. 3.9), but reliable estimates could not be produced for adult female long-eared chipmunks.

Survival in yellow-pine chipmunks was influenced by development and disturbance, as well as group affiliation and sampling year (Table 3.6). Adult survival rates were greater than juvenile survival rates, and annual survival was greater between 2003 and 2004 than between 2004 and 2005 for all groups (Fig. 3.10). Development at the 300m scale had a pronounced negative impact on adult survival in yellow-pine chipmunks (Fig. 3.11). Although juvenile survival rates were much lower than adult survival in general (Fig. 3.10), the negative relationship with development was weaker for juveniles than that for adults (Fig. 3.11). Disturbance in the form of frequency of dogs at the site also influenced survival more so for adults than juveniles ($\beta_{DOGS} = -0.2451$, $SE_{DOGS} = 0.1267$; Table 3.6). The impact of lower annual survival between 2004 and 2005 is shown by the dramatic decrease in adult population size in 2005 (Fig. 3.10).

Sampling year was the most important factor affecting shadow chipmunk survival, but development at the 1000m scale and disturbance also affected survival (Table 3.7). Development had a negative effect on survival (Figure 3.12), while disturbance in the form of dog and human use positively impacted survival (Figure 3.13 and 3.14). In contrast, survival rates in the lodgepole chipmunk were negatively related to both disturbance factors (Figure 3.15 and 3.16), as well as to development at the 300m scale (Figure 3.17; Table 3.8).

Sex and age were important factors affecting ground squirrel survival and emigration (Table 3.9 and 3.19). For California ground squirrels, development at the 300m scale was the most influential covariate affecting these parameters (Figure 3.18 and 3.15). Development had a significant negative impact on California ground squirrel survival ($\beta_{D300} = -0.9360$, $SE_{D300} = 0.3711$; Fig. 3.19), and survival rates for females were greater than male survival rates (Fig. 3.16). Age was the most important factor affecting emigration-immigration rates in California ground squirrels (Table 3.9, Fig. 3.19), with juveniles exhibiting a much greater propensity for dispersal than adults. The slightly positive relationship between development and emigration-immigration rate was minimal ($\beta_{D300} = 0.1075$, $SE_{D300} = 0.8373$; Fig. 3.17).

Age was the most important factor affecting golden-mantled ground squirrel survival (Table 3.10) with adults exhibiting much higher survival rates overall than juveniles (Figure 3.14). However, development at the 1000m scale did have an important negative impact on adult survival rates (Fig. 3.20). Again, emigration-immigration was facilitated by development in golden-mantled ground squirrels, with emigration-immigration rates increasing with increasing development at the 1000m scale (Fig. 3.21). Males of this species were more likely to emigrate than females.

Douglas squirrels were not captured frequently enough across years to estimate emigration-immigration rates. However, development at the 300m and 1000m scales negatively influenced Douglas squirrel survival rates (Table 3.24, Fig. 3.22). Shifts in population size were best explained by year and by adult-juvenile and male-female status (Table 3.24).

Our estimates of population parameters for squirrels and chipmunks basin showed that population size, survival rates and emigration-immigration rates varied by species, age, sex and year. As one would expect, adults had higher survival rates and lower emigration rates than juveniles in all cases where parameter estimates could be generated. Similarly, males had lower survival rates and higher emigration-immigration rates than females. The highest survival estimates were for the ground squirrels and the two larger-bodied chipmunk species (long-eared and shadow chipmunk), while the lowest survival estimates were for the lodgepole chipmunk and the Douglas squirrel. For chipmunk species, sampling year was an important explanatory factor impacting survival, and low annual survival between 2004 and 2005 was followed by a dramatic decrease in adult population sizes of long-eared and yellow-pine chipmunks in the summer of 2005. This suggests that region-wide factors (e.g. weather, resource availability) were affecting annual survival in these species.

Table 3.5. Top ten models for the long-eared chipmunk based on AICc rank showing the importance of time (t, y), age and sex (g), development and disturbance on survival (S), emigration (G), capture probability (P), and abundance (N).

Rank	Model Parameterization	AICc	Delta AICc	AICc Weights	Model Likelihood	k	Deviance
1	{S(t),G(g+D1000),P(g*y),N(g*t)}	2485.18	0	0.43262	1	30	2424.41
2	{S(t+D1000),G(g+D1000),P(g*y),N(g*t)}	2486.46	1.2721	0.22902	0.5294	31	2423.63
3	{S(t),G(g+D300),P(g*y),N(g*t)}	2488.40	3.211	0.08687	0.2008	30	2427.62
4	{S(t+PEOPLE),G(g+PEOPLE),P(g*y),N(g*t)}	2489.32	4.1362	0.05469	0.1264	31	2426.50
5	{S(t),G(age+D1000),P(g+y),N(g*t)}	2489.52	4.3323	0.04959	0.1146	23	2443.06
6	{S(t+D300),G(g+D300),P(g*y),N(g*t)}	2490.04	4.8558	0.03817	0.0882	31	2427.22
7	{S(t),G(g+PEOPLE),P(g*y),N(g*t)}	2490.12	4.9331	0.03672	0.0849	30	2429.35
8	{S(t+PEOPLE),G(age+PEOPLE),P(g+y),N(g*t)}	2491.07	5.8877	0.02278	0.0527	23	2444.62
9	{S(t+D1000),G(age),P(g+y),N(g*t)}	2492.67	7.4836	0.01026	0.0237	23	2446.21
10	{S(t+DOGS),G(g+DOGS),P(g*y),N(g*t)}	2492.69	7.5037	0.01016	0.0235	31	2429.86

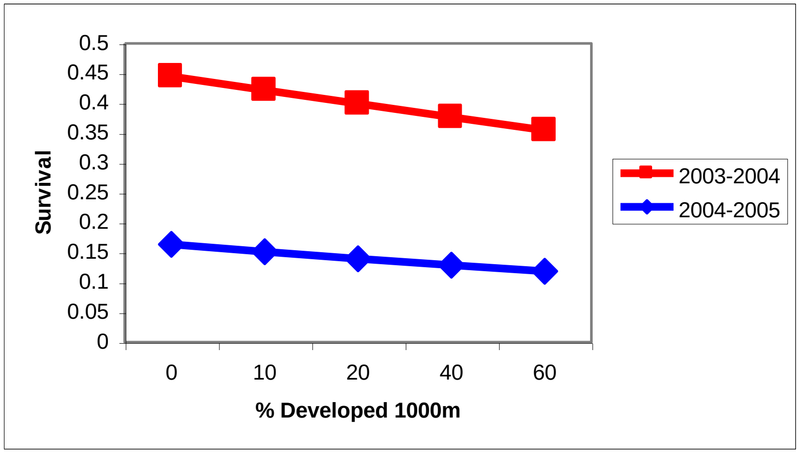


Figure 3.8. Functional relationship between estimated annual survival rate and development at the 1000m spatial scale for long-eared chipmunks based on the second ranked model.

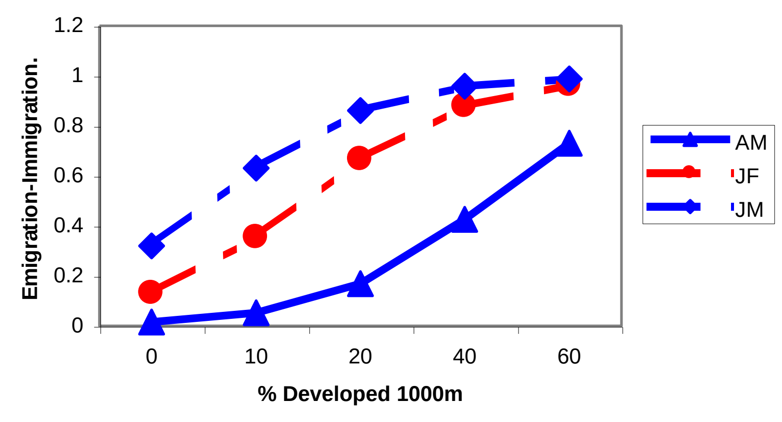


Figure 3.9. Functional relationship between estimated emigration rates and development at the 1000m spatial scale for long-eared chipmunks. Parameter estimates for female survival could not be obtained for this species. Adult male (AM), juvenile female (JF) and juvenile male (JM) estimates from the top-ranked model are presented.

Table 3.6. Top ten models for the yellow-pine chipmunk based on AICc rank showing the importance of time (t), age and sex (g), development and disturbance on survival (S), capture probability (P), and abundance (N). Models were not able to produce valid estimates for the emigration parameter, G, so this parameter was fixed at ‘0’ to reduce model complexity and obtain reliable estimates for the remaining parameters.

Rank	Model Parameterization	AICc	Delta AICc	AICc Weights	Model Likelihood	k	Deviance
1	{S(g+t+D300),G(0),P(g+t),N(g*t)}	2585.25	0	0.28547	1	51	2481.19
2	{S(g+t+DOGS),G(0),P(g+t),N(g*t)}	2586.28	1.0345	0.17018	0.5961	51	2482.22
3	{S(g+t+D500),G(0),P(g+t),N(g*t)}	2586.59	1.3366	0.14632	0.5126	51	2482.52
4	{S(g+t+D100),G(0),P(g+t),N(g*t)}	2587.39	2.1425	0.0978	0.3426	51	2483.33
5	{S(g+t+D1000),G(0),P(g+t),N(g*t)}	2587.87	2.6223	0.07694	0.2695	51	2483.81
6	{S(g+t+PEOPLE),G(0),P(g+t),N(g*t)}	2587.88	2.6301	0.07664	0.2685	51	2483.82
7	{S(g+t),G(0),P(g+t),N(g*t)}	2588.09	2.8403	0.06899	0.2417	50	2486.11
8	{S(g+D300),G(0),P(g+t),N(g*t)}	2589.23	3.9802	0.03902	0.1367	50	2487.25
9	{S(g),G(0),P(g+t),N(g*t)}	2591.81	6.5585	0.01075	0.0377	49	2491.90
10	{S(age+d300),G(0),P(g+t+y),N(g*t)}	2592.36	7.1127	0.00815	0.0285	28	2535.74

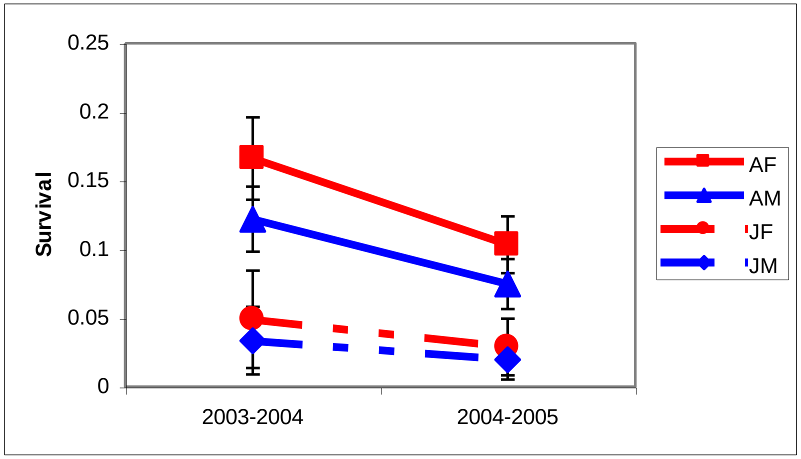


Figure 3.10. Parameter estimates for adult female (AF), adult male (AM), juvenile female (JF) and juvenile male (JM) annual survival rate in yellow-pine chipmunks.

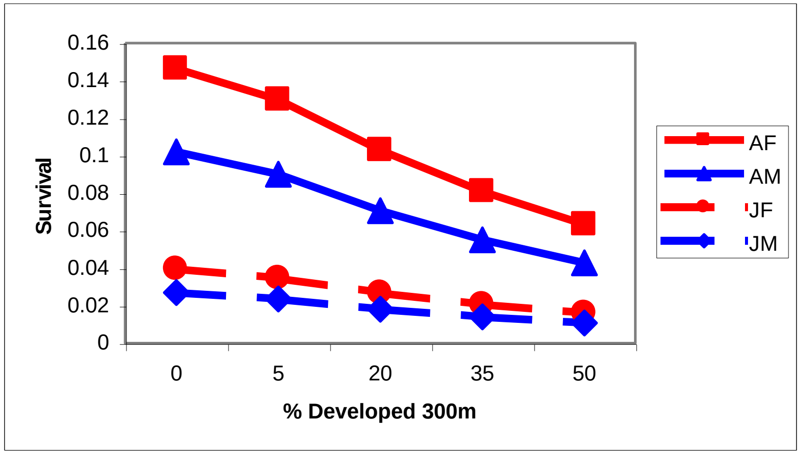


Figure 3.11. Functional relationship between annual survival and development at the 300m spatial scale for adult female (AF), adult male (AM), juvenile female (JF) and juvenile male (JM) yellow-pine chipmunks under the top-ranked model.

Table 3.7. Top ten models for the shadow chipmunk based on AICc rank showing the importance of year (t, y), age, sex, development and disturbance on survival (S) and capture probability (P). Models were not able to produce valid estimates for the emigration parameter, G, so this parameter was fixed at ‘0’ to reduce model complexity and obtain reliable estimates for the remaining parameters.

Rank	Model Parameterization	AICc	Delta AICc	AICc Weights	Model Likelihood	k	Deviance
1	{S(t),G(0),P(age+t*y),N(.)}	795.30	0	0.23091	1	29	731.48
2	{S(t+D1000),G(0),P(age+t*y),N(.)}	795.64	0.3373	0.19508	0.8448	30	729.40
3	{S(t+DOGS),G(0),P(age+t*y),N(.)}	795.69	0.3821	0.19076	0.8261	30	729.44
4	{S(t+PEOPLE),G(0),P(age+t*y),N(.)}	795.75	0.4452	0.18483	0.8004	30	729.51
5	{S(t+D100),G(0),P(age+t*y),N(.)}	797.31	2.0103	0.08451	0.366	30	731.07
6	{S(t+D300),G(0),P(age+t*y),N(.)}	797.61	2.3013	0.07307	0.3164	30	731.36
7	{S(age+D1000),G(0),P(age+t*y),N(.)}	800.70	5.4	0.01552	0.0672	30	734.46
8	{S(age),G(0),P(age+t*y),N(.)}	801.11	5.8018	0.01269	0.055	29	737.29
9	{S(sex),G(0),P(age+t*y),N(.)}	801.12	5.8196	0.01258	0.0545	29	737.30
10	{S(sex),G(0),P(sex+t*y),N(.)}	813.36	18.054	0.00003	0.0001	29	749.54

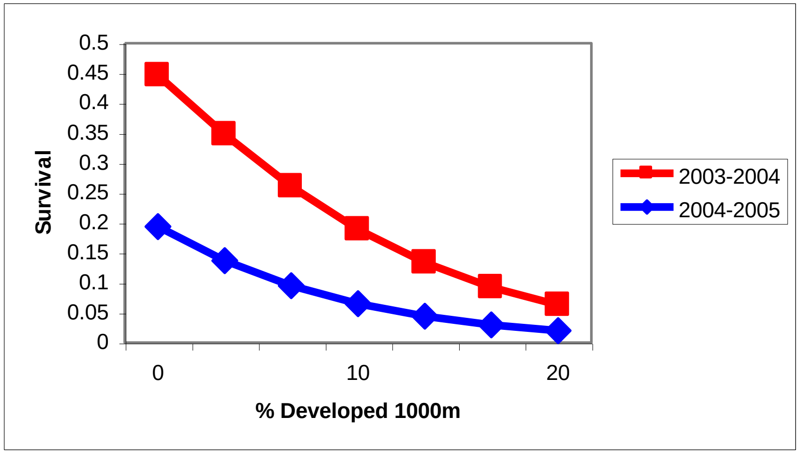


Figure 3.12. Functional relationship between estimated over-winter survival rate and development at the 1000m spatial scale for shadow chipmunks based on the second ranked model.

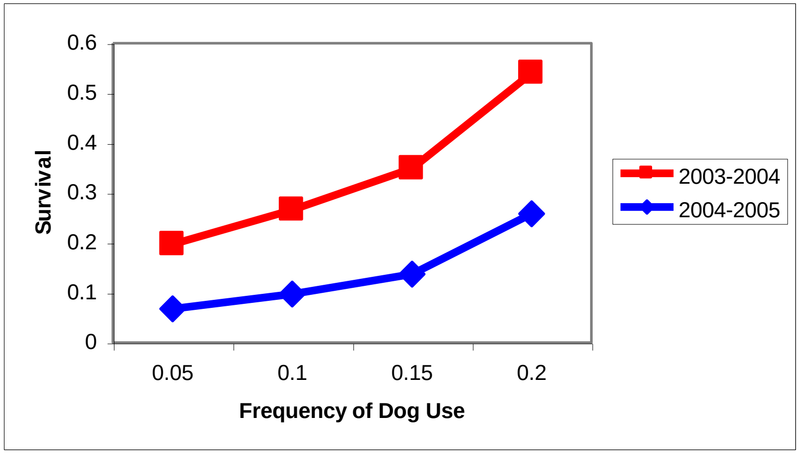


Figure 3.13. Functional relationship between annual survival in shadow chipmunks and frequency of dog use under the third-ranked model.

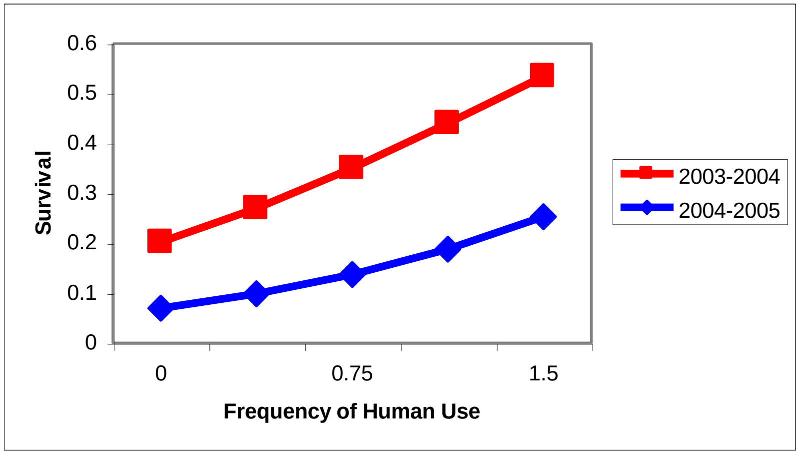


Figure 3.14. Functional relationship between annual survival in shadow chipmunks and frequency of human use under the fourth-ranked model.

Table 3.8. Top ten models for the lodgepole chipmunk based on AICc rank showing the importance of disturbance and development on survival (S) as well as the influence of time on capture probability (P). Models were not able to produce valid estimates for the emigration parameter, G, so this parameter was fixed at ‘0’ to reduce model complexity and obtain reliable estimates for the remaining parameters. The population estimates were also not valid, so the population parameter was reduced to a “dot” model for purposes of addressing hypotheses concerning the influence of development and disturbance.

Rank	**Model Parameterization**	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**k**	**Deviance**
1	{S(.+DOGS),G(0),P(t),N(.)}	364.18	0	0.20547	1	10	341.91
2	{S(.),G(0),P(t),N(.)}	364.23	0.0492	0.20048	0.9757	9	344.40
3	{S(.+D300),G(0),P(t),N(.)}	364.94	0.7567	0.14075	0.685	10	342.67
4	{S(.+PEOPLE),G(0),P(t),N(.)}	365.18	0.9969	0.12482	0.6075	10	342.91
5	{S(.+D1000),G(0),P(t),N(.)}	365.61	1.4303	0.1005	0.4891	10	343.35
6	{S(sex),G(0),P(t),N(.)}	366.34	2.1614	0.06973	0.3394	10	344.08
7	{S(age),G(0),P(t),N(.)}	366.36	2.1817	0.06902	0.3359	10	344.10
8	{S(.+D100),G(0),P(t),N(.)}	366.53	2.3502	0.06345	0.3088	10	344.27
9	{S(age),G(0),P(g+t),N(.)}	368.83	4.6476	0.02012	0.0979	11	344.08
10	{S(age),G(0),P(g+t),N(g)}	371.36	7.1783	0.00568	0.0276	12	344.08

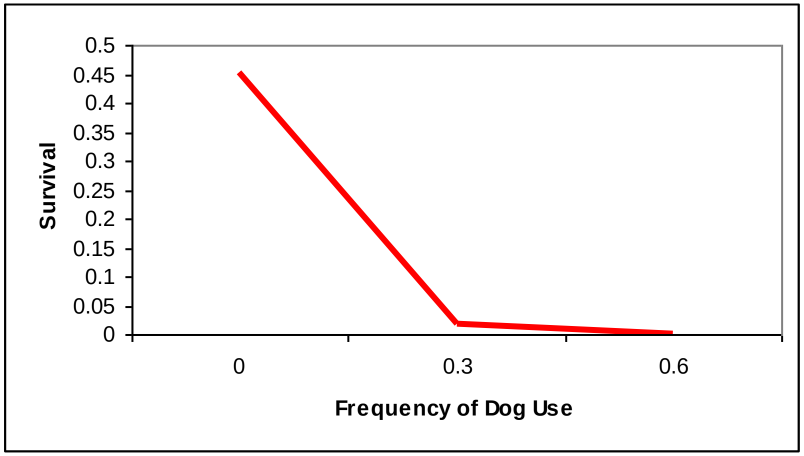


Figure 3.15 Functional relationship between the estimated annual survival rate and frequency of dog use for lodgepole chipmunks based on the top-ranked model.

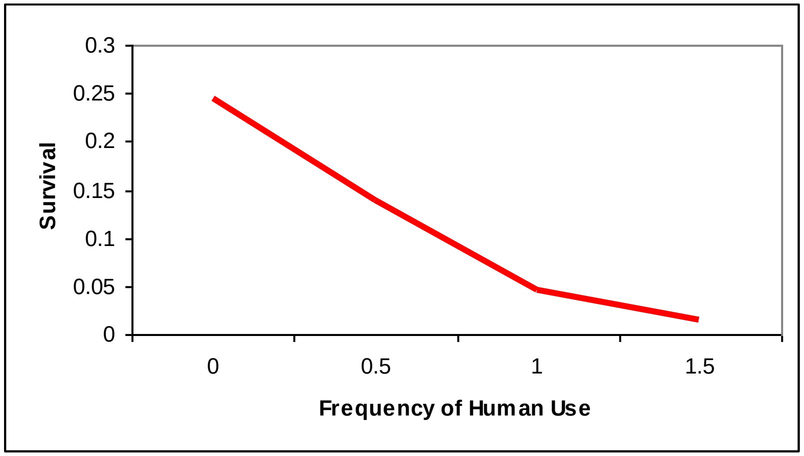


Figure 3.16. Functional relationship between annual survival in lodgepole chipmunks and frequency of human under the fourth-ranked model.

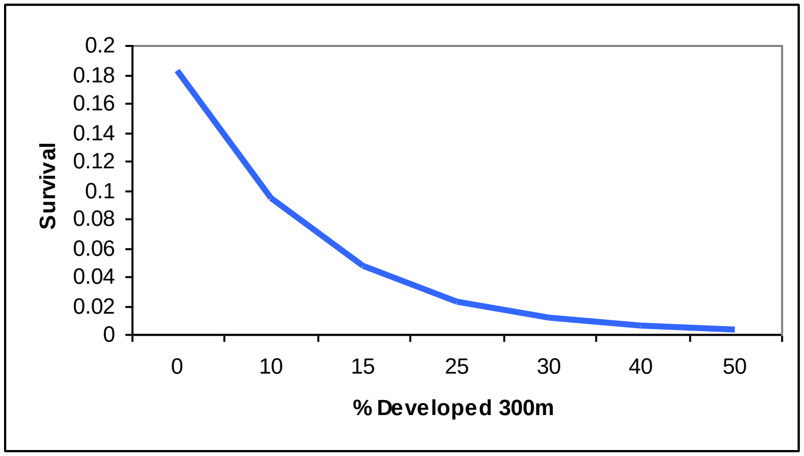


Figure 3.17. Functional relationship between annual survival in lodgepole chipmunks and development at the 300m spatial scale under the third-ranked model.

Table 3.9. Top ten models for the California ground squirrel based on AICc rank showing the importance of sex, age, development and disturbance on survival (S) and emigration (G), as well as the importance of group (g), sampling occasion (t) and year (y) on capture probability (P) and abundance (N).

Rank	Model Parameterization	AICc	Delta AICc	AICc Weights	Model Likelihood	k	Deviance
1	{S(sex+D300),G(age),P(g+t+y),N(g*t)}	1541.88	0	0.54865	1	30	1479.50
2	{S(sex+D300),G(age+D300),P(g+t+y),N(g*t)}	1544.02	2.1453	0.1877	0.3421	31	1479.48
3	{S(sex+D1000),G(age),P(g+t+y),N(g*t)}	1544.73	2.8525	0.13179	0.2402	30	1482.35
4	{S(sex+D100),G(age),P(g+t+y),N(g*t)}	1545.78	3.9064	0.07781	0.1418	30	1483.40
5	{S(sex+PEOPLE),G(age),P(g+t+y),N(g*t)}	1548.20	6.3201	0.02328	0.0424	30	1485.82
6	{S(sex+DOGS),G(age),P(g+t+y),N(g*t)}	1548.38	6.5024	0.02125	0.0387	30	1486.00
7	{S(sex),G(age),P(g+t+y),N(g*t)}	1550.04	8.1593	0.00928	0.0169	29	1489.81
8	{S(t),G(age),P(g+t+y),N(g*t)}	1558.55	16.6707	0.00013	0.0002	29	1498.32
9	{S(age),G(age),P(g+t+y),N(g*t)}	1558.92	17.0404	0.00011	0.0002	28	1500.84
10	{S(age),G(0),P(g+t+y),N(g*t)}	1567.01	25.1298	0	0	27	1511.08

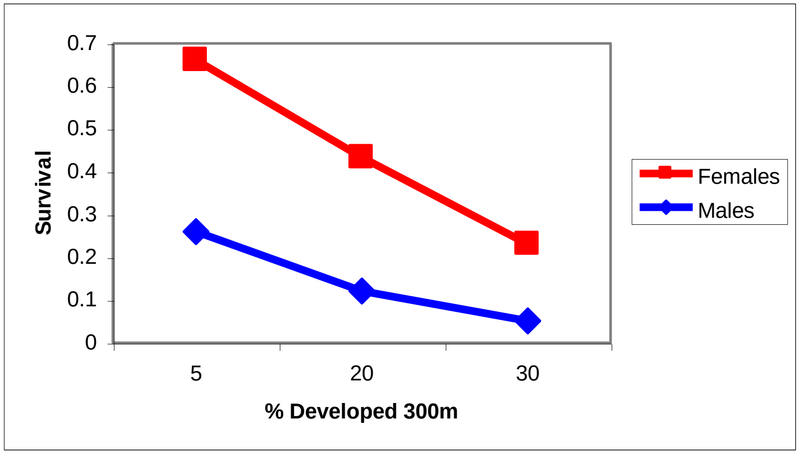


Figure 3.18. Functional relationship between estimated annual survival rate and development at the 300m spatial scale for California ground squirrels based on the top ranked model.

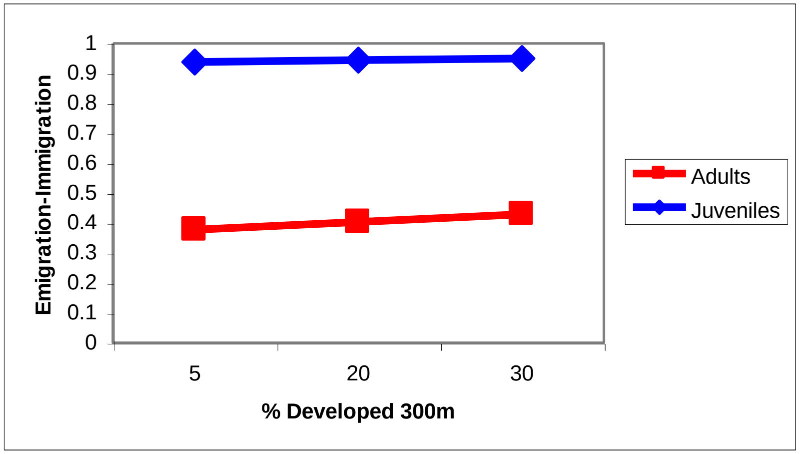


Figure 3.19. Functional relationship between emigration rate and development at the 300m spatial scale for California ground squirrels based on the second ranked model.

Table 3.10. Top ten models for the golden-mantled ground squirrel based on AICc rank showing the importance of age, sex and development on survival (S) and emigration (G), as well as the importance of group (g) and sampling occasion (t) on capture probability (P) and age on abundance (N).

Rank	Model Parameterization	AICc	Delta AICc	AICc Weights	Model Likelihood	k	Deviance
1	{S(age),G(sex),P(g+t),N(age)}	1271.94	0	0.17223	1	17	1236.77
2	{S(age+D1000),G(sex),P(g+t),N(age)}	1272.40	0.4597	0.13687	0.7947	18	1235.09
3	{S(age),G(sex+D1000),P(g+t),N(age)}	1273.55	1.6058	0.07717	0.4481	18	1236.24
4	{S(age+D300),G(sex),P(g+t),N(age)}	1273.60	1.6593	0.07513	0.4362	18	1236.29
5	{S(age),G(sex+D300),P(g+t),N(age)}	1273.68	1.742	0.07209	0.4186	18	1236.37
6	{S(age+D100),G(sex),P(g+t),N(age)}	1273.75	1.8117	0.06962	0.4042	18	1236.44
7	{S(age),G(sex+DOGS),P(g+t),N(age)}	1273.82	1.881	0.06725	0.3905	18	1236.51
8	{S(age+DOGS),G(sex),P(g+t),N(age)}	1273.91	1.9657	0.06446	0.3743	18	1236.60
9	{S(age),G(sex+PEOPLE),P(g+t),N(age)}	1274.07	2.1268	0.05947	0.3453	18	1236.76
10	{S(age+PEOPLE),G(sex),P(g+t),N(age)}	1274.08	2.1389	0.05911	0.3432	18	1236.77

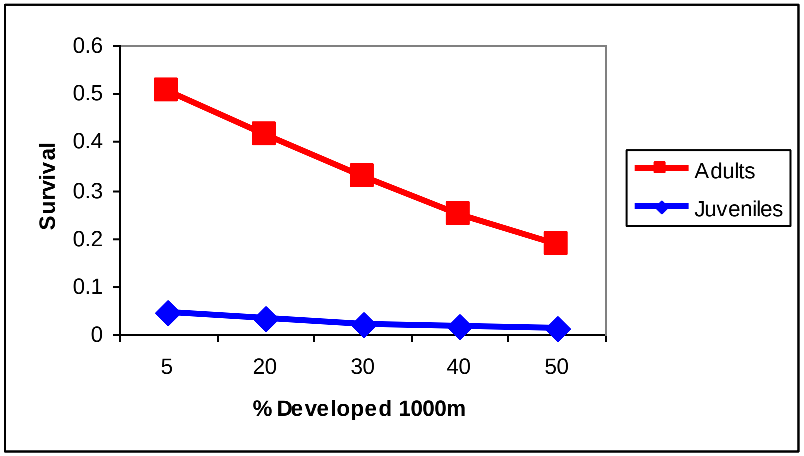


Figure 3.20. Functional relationship between estimated annual survival rate and development at the 1000m spatial scale for golden-mantled ground squirrels based on the second ranked model.

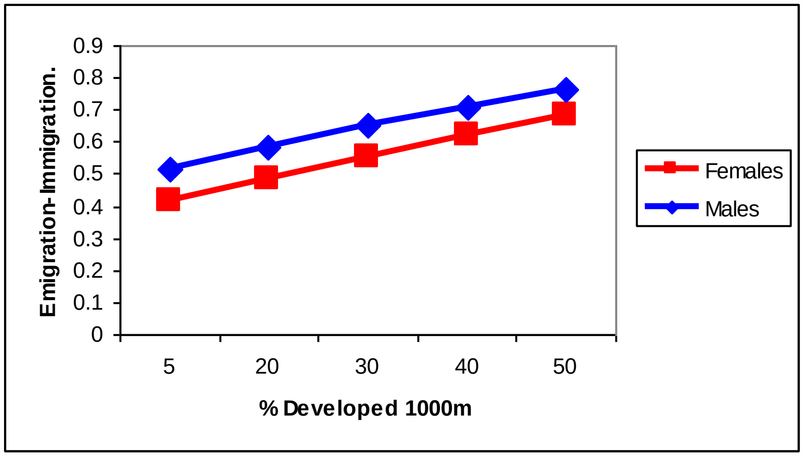


Figure 3.21. Functional relationship between emigration rate and development at the 1000m spatial scale for golden-mantled ground squirrels based on the third ranked model.

Table 3.11. Top ten models for the Douglas squirrel based on AICc model weight showing the importance of development on survival (S), as well as the importance of sampling occasion (t) on capture probability (P) and sex and age (g) and year (t) on abundance (N).

Rank	Model Parameterization	AICc	Delta AICc	AICc Weights	Model Likelihood	k	Deviance
1	{S(.+D300),G(0),P(t),N(g*t)}	751.47	0	0.22843	1	22	704.55
2	{S(.+D1000),G(0),P(t),N(g*t)}	751.49	0.0263	0.22545	0.9869	22	704.58
3	{S(.),G(0),P(t),N(g*t)}	752.27	0.8014	0.15302	0.6699	21	707.61
4	{S(t+D300),G(0),P(t),N(g*t)}	753.14	1.6779	0.09872	0.4322	23	703.95
5	{S(.+DOGS),G(0),P(t),N(g*t)}	753.97	2.5041	0.06531	0.2859	22	707.05
6	{S(t),G(0),P(t),N(g*t)}	754.09	2.6229	0.06155	0.2694	22	707.17
7	{S(sex),G(0),P(t),N(g*t)}	754.16	2.6949	0.05937	0.2599	22	707.25
8	{S(.+D100),G(0),P(t),N(g*t)}	754.18	2.717	0.05872	0.2571	22	707.27
9	{S(.+PEOPLE),G(0),P(t),N(g*t)}	754.53	3.0619	0.04942	0.2163	22	707.61
10	{S(.),G(0),P(g),N(g*t)}	771.76	20.296	0.00001	0	17	736.02

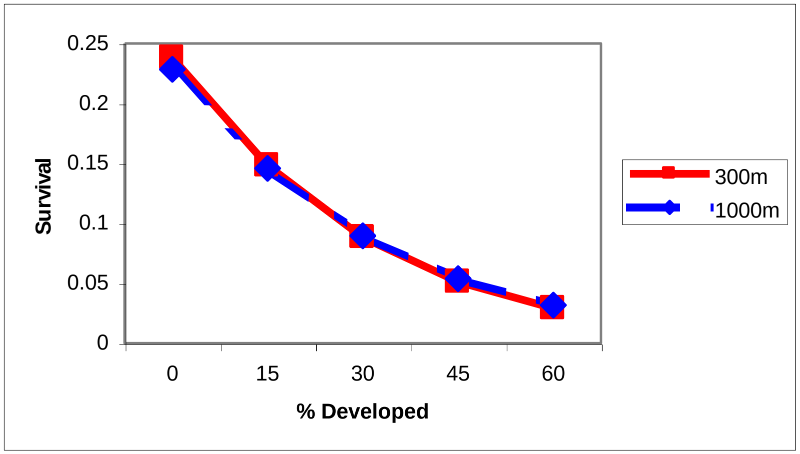


Figure 3.22. Functional relationship between survival and development at two spatial scales for Douglas squirrel.

Discussion

We found that patterns of total species richness and relative abundance in the Lake Tahoe basin were not greatly influenced by urban development and associated disturbance. Small mammal species are relatively abundant in the forests of Lake Tahoe, and the retention of elements of native forest even within more developed areas of Tahoe is likely to retain higher populations than would otherwise occur in developed areas.

The weak unimodal influence of development on abundance could be due to greater disturbance frequency and/or intensity at developed when compared to undeveloped sites. Since the most important factor influencing the diversity and distribution of many small mammal species is habitat structure (Lawlor 2003) and habitat structure in forest systems is shaped largely by disturbance. Disturbance can create new habitat conditions or it may reduce the number of individuals of a particular species, thereby allowing other species to colonize and exploit new habitats (Reice 2005). Development can also change the dominance structure of communities, where generalist species can dominate the community. Urban development near a site may be creating an intermediate disturbance pattern (Connell 1978) that allows more species to persist at a single location. In addition, the relatively predictable disturbance frequency and intensity in highly managed urban landscapes may actually provide a certain level of habitat stability that allows these species to maintain higher overall population sizes. However, the abundance pattern exhibited by the herbivore group indicates that development can reach a threshold where disturbance intensity/frequency can exceed the optimal level.

It is most likely that changes in abundance affected changes in detectability, thus altering richness estimates among years. Species have a higher probability of detection when they are abundant. Indeed, higher richness coincided with an overall increase in the estimated population size of chipmunks, golden-mantled ground squirrels and Douglas squirrels from 2003 to 2004, followed by a decrease in both species richness and population size in 2005. Each of these species relies on pine cone seeds as a major food resource (Van Dersal 1938; Smith 1943; Tevis 1952, 1953; Grinnell & Dixon 1918; Gordon 1943; Hoffmeister 1986; Steele 1999; Lawlor 2003); therefore, it is possible that their populations may be following fluctuations in cone production among years (Smith 1970; Buchanan *et al* 1990). In turn, an increase in overall abundance would increase detectability, which would result in more species being detected per site in 2004 relative to the other two years.

In addition to urban development surrounding sites, the percent cover of bare ground at the site was an important factor that was positively associated with both species richness and abundance. Bare ground on the forest floor is a likely consequence of ground-level disturbance removing litter and preventing plant germination. Such a pattern of clearing may simulate conditions typical of early successional communities. Since many forest species have adapted to use early successional habitats, disturbance that increases the amount of bare ground at a site may allow species associated with earlier seral conditions to persist at sites where they may not otherwise. Species we found at our sites that are often found in newly disturbed stands include voles, jumping mice and deer mice (Hallett & O'Connell 1997). The fact that small mammal species richness and abundance are positively related to the amount of urban development and the amount of bare ground indicates that the impacts of disturbance in urban lots may be similar in effect to natural disturbance regimes that facilitate species coexistence and productivity.

Another form of disturbance experienced by Lake Tahoe basin species is the presence of humans and domestic dogs. We found that human disturbance had variable effects on small mammal species. While the frequency of use by people was found to be positively associated with species richness, there was a negative relationship between total relative abundance and human use. Since the species detected in the highest numbers at all sites were ground squirrels and chipmunks, this pattern may be a reflection of a negative effect of human disturbance on these species in particular. Ground squirrels and chipmunks are diurnal and primarily terrestrial. Since human activity occurs mostly during the day and at ground level, it is very likely that these species are negatively affected by human activity. In turn, a decrease in the abundance of numerically dominant species might allow other less abundant species to occupy an area.

In the case of domestic dogs, we found that their presence was positively associated with tree squirrel abundance. While dogs could potentially harass and prey on rodents, their presence did not have a negative impact on arboreal squirrel relative abundance. In fact, it may be that the presence of dogs actually deters more efficient predators of these squirrels. Since Douglas squirrels spend much of their time in trees, they are often inaccessible prey items for terrestrial predators such as dogs and coyotes. However, mustelid predators (including members of the weasel family) that are adept at climbing may actually be deterred by the presence of dogs. Therefore, domestic dogs may provide some degree of protection from predation for tree squirrels, allowing them to persist in higher numbers.

While development and disturbance influenced Lake Tahoe basin small mammals, we also found that habitat heterogeneity (i.e., the number of different CWHR habitat types) surrounding sites had a substantial positive effect on species richness. Since many of the forest-dwelling small mammal species are sympatric and have similar resource requirements, they assort based on microhabitat or dietary differences (Lawlor 2003), adaptations that evolved in the heterogeneous landscape created by natural forest disturbance dynamics. Heterogeneous landscapes offer a greater diversity of resources, both spatially and temporally, which increases animal diversity (Rosenzweig & Abramsky 1993). Therefore, maintaining adequate levels of habitat diversity at the landscape scale will be important for maintaining species diversity.

The species identified by this study that may be most vulnerable to habitat alteration and development in the basin are shadow chipmunks, lodgepole chipmunks and shrews. These species exhibited a distribution threshold with respect to urbanization and were not detected at sites that exceeded moderate levels of development or disturbance. For these species, habitat quality may be adversely impacted by development and/or disturbance. Shrews composed the only functional group where specific habitats were identified as important factors associated with relative abundance. For shrews, a combination of Sierran mixed conifer and white fir habitat both at and adjacent to the site positively affected relative abundance. In addition, the amount of montane riparian and red fir / subalpine conifer habitat at as site positively influenced abundance. Previous research has also found Trowbridge’s shrew to be associated with fir forests, typically with a dry forest floor (Dalquest 1948; George 1988), and in the central and southern Sierra they are likewise most abundant in the mixed conifer vegetation zone (Verner & Boss 1980). This indicates that shrews are habitat specialists that depend on relatively few specific habitat types. If urban development degrades important habitats for the species we identified here as sensitive to development and disturbance, then an overall decrease in their distribution and abundance may result.

We found that population dynamics of squirrels and chipmunks were adversely affected by urban development. The degree of response varied among these species, but the evidence was consistent across all species: survival rates decreased and emigration rates increased as development pressure increased. The fact that survival was negatively impacted by development is an indication that habitat conditions in urban areas maybe degraded. Furthermore, a higher propensity of individuals to move into and out of urban sites has negative implications, because when individuals disperse mortality risk increases, particularly if the matrix between habitat fragments proves to be inhospitable (Ray 2005). Therefore, maintaining patches of forest habitat within the urban matrix is important for facilitating successful dispersal and ultimately sustaining interconnected populations of small mammal species.

Understanding how the distribution and abundance of small mammal species influences forest function and biodiversity has economic and conservation implications beyond the relevance of basic ecological inquiry. Small mammals are an integral part of the forest ecosystem, and the role of small mammals in forest dynamics is multifaceted and complex. Small mammals are an essential component of forest food webs and play an important part in the reproductive life history of many forest plants. The association of small mammals with other forest species has both direct and indirect effects on forest health and regeneration, biodiversity and ecosystem function (Sullivan *et al* 1993, Maser *et al* 1978, McShea 2000, Sirotnak & Huntly 2000). Therefore, identifying the nature of species' distributions and community structure helps to direct the study of population dynamics within the system and elucidate the mechanisms of community organization. It is important to consider these factors when making predictions about the impacts of future management and development.

We identified several important explanatory factors that influence small mammal species richness and abundance in the Lake Tahoe basin. Urban development and disturbance positively affected species richness and abundance in some species, as did habitat variables such as percent cover of bare ground and overall habitat heterogeneity. However, it is very possible that the pattern of higher species richness and abundance in urban areas is not indicative of habitat suitability or quality. Instead it may be an early warning sign that this ecosystem is suffering the negative impacts of habitat fragmentation. When habitat is fragmented and/or degraded remnant patches are expected to initially support a greater number of species and overall abundance as individuals are packed into smaller and smaller patches of suitable habitat (Collinge & Forman 1998). Over time, species are lost and the ecological community is degraded (Johnson & Klemens 2005). The altered primary population processes we identified are another important sign that small mammals in the Lake Tahoe basin are in the midst of ecological decay (Collinge & Forman 1998). If development pressure and disturbance increases, habitat conditions may decline to a point that exceeds the capacity of some species to persist (Reice 2005).

While most forest-associated species in the Lake Tahoe basin do not appear to have reached a distribution threshold with respect to urban development, maintaining landscape linkages may be crucial to preventing loss of species. The parks and open space in the basin today may be able to maintain representative samples of species and habitats; however, they may not be sufficient to maintain ecologically functional landscapes. If population processes are being negatively impacted by development as we found here, then remnant habitat patches may not be able to maintain sustainable populations. Furthermore, if the matrix surrounding habitat patches becomes increasingly inhospitable to a level that it presents a dispersal barrier, then populations can become effectively isolated and species may be lost. Maintaining stable population dynamics in addition to interconnected populations of forest-associated species will be important in preserving basin biodiversity and will set the course for the forest community that will be realized in the future.

Chapter 4: Large Mammals

Introduction

A wide array of larger-bodied mammals is associated with forested habitats in the Lake Tahoe basin. Many of these larger native species may be expected to be sensitive to development and habitat modification because of large home range requirements and resulting smaller population densities compared to smaller-bodied species. However, some of the less specialized species, such as black bear (*Ursus americana*), coyote (*Canis latrans*), and black-tailed deer (*Odocoileus hemionus*) may respond positively to low to intermediate levels of development in terms of increased population densities and increased reproductive success. In addition, some of these species may be attracted to certain attributes in the surrounding urban matrix and, as a result, may come into conflict with humans. Species of particular public and/or management significance in this group include: coyote, marten (*Martes americana*), mule deer and black bear. The marten, black bear, and coyote are among the top predators in the Lake Tahoe basin. Other species in this group include: spotted skunk (*Spilogale putoris*), long-tailed weasel (*Mustela frenata*), a variety of tree and ground squirrels, chipmunks, domestic dog (*Canis familiaris*), and domestic cat (*Felis cattus*). The objectives for medium to large mammals are to use detection and visitation data to examine the effects of development and human activity on the distribution, community composition, frequency of use and species richness.

Methods

Data Collection

Medium to large-bodied mammals were surveyed using a combination of track and photographic surveys and pellet-group counts. Track surveys were conducted using enclosed sooted aluminum track plates (Barrett 1983, Fowler 1995, Zielinski and Kucera 1995). Photographic evidence of species presence was collected using remotely triggered cameras (Zielinski and Kucera 1995). Use of multiple techniques may also improve the probability of detecting resident animals as responses to the track plates and cameras may differ (Campbell, unpublished data). Some larger carnivores like coyotes and bobcats may be reluctant to enter enclosed track plates given the relatively low height of the plastic canopy (opening height 27.5 cm) although others, such as black bears, appear undeterred. Further, photographic evidence provides a reliable means by which to distinguish coyote and bobcat detections from those of domestic dogs and cats, which is not possible from tracks due to the overlap in track size. The presence of deer and leporids such as snowshoe hare may not be adequately sampled using the above methods. To better describe their distributions, pellet-group counts (Smith 1968, Krebs et al. 1987, McKelvey et al. 2002) were used. Each sample unit consisted of a total of 4 enclosed track plates, 2 remote cameras, and 4 pellet-group plot arrays.

Track and Camera Surveys

An array was established centered on the identified sample unit center. One track plate station (TP1) was placed near the sample unit center. One camera (TM1) was located 100m from TP1 on a randomly selected azimuth. Three track stations were placed at a distance of approximately 250 m from the center at 0º (TP2), 120º (TP3), and 240º (TP4; Fig. 5.1). One of the three outer track plate stations was randomly selected to be paired with a remote camera (TM2), which was established 100 m from the track plate station on a randomly chosen azimuth. All devices (track plate stations and cameras) were established a minimum of 30 m from a patch edge or trail/road. Track plates and cameras were baited with chicken (drummettes for track plates, half chickens for cameras) and baby carrots, and a commercial scent was used as a lure.

Track plates and cameras were visited every two days for a total of five visits. A species was determined to be present in a sample unit if any device within the sample unit recorded a detection during the survey period. The type of data derived from these methods include: species detected/not detected, species identity (species or genus level), date of visit, frequency of visitation, and time of visit (cameras). The response variables include species detected/not detected, species richness, and frequency of use. Frequency of visitation to detection devices within a patch may be used to represent the intensity of patch use (Gehring et al. 2003).

Pellet-group Counts

At random distances along the transect between track plate stations, pellet-group count plot arrays were established 10 m off the transect (Fig. 4.1). The array consisted of four plots, one in each cardinal direction at a distance of 5 m. Each plot had a radius of approximately 1.7 m to yield a plot area of approximately 9.3 m^2. A total of 16 plots (4 plots in each of 4 arrays) were established for each sample unit. Pellet-group counts occur once near the beginning of the sampling period for each sample unit. The data recorded were species detected/not-detected. Although the number of pellets /unit area has been used to derive an index of species density in other studies, the index is sensitive to the defecation rate used (number of pellets/individual), which appears to be location-specific (Fuller 1991).

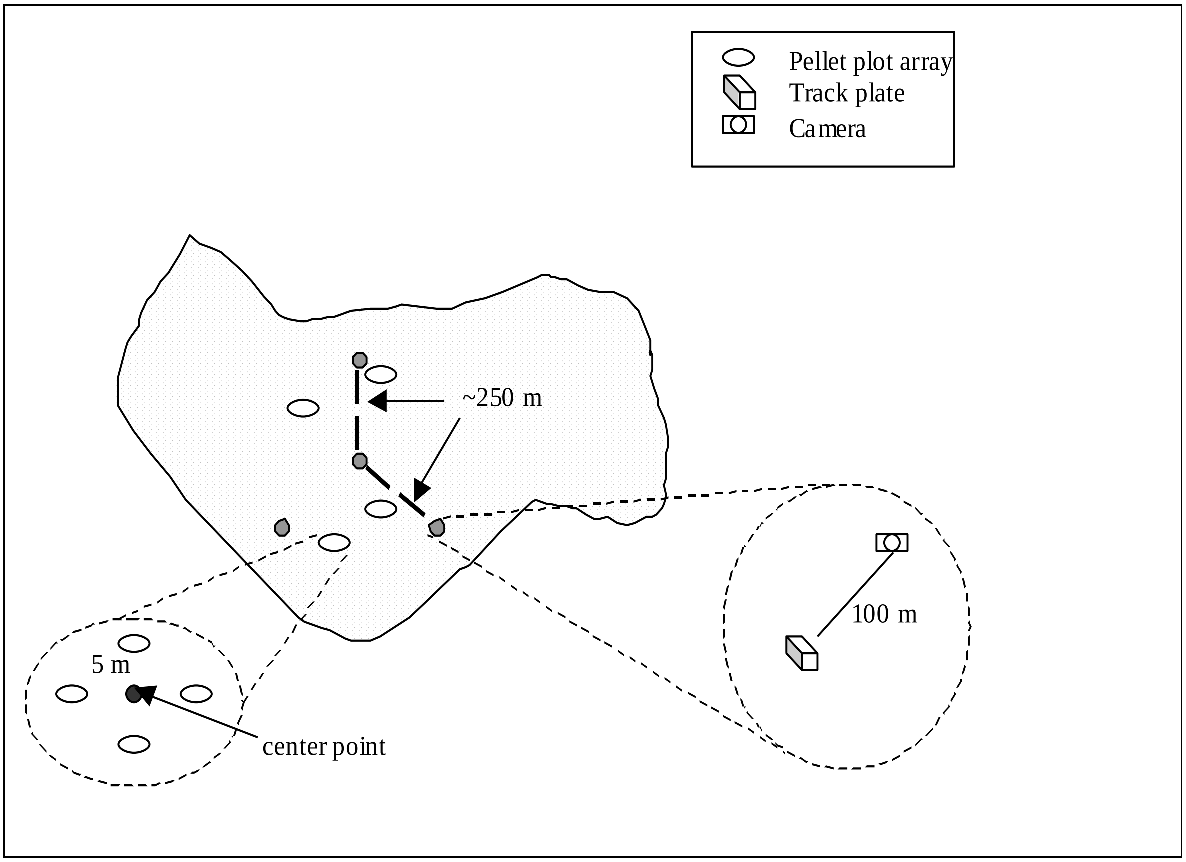


Figure 4.1. Schematic of the arrangement of survey devices and plots. One camera was paired with the track plate at the center point and the other was randomly paired with one of the remaining track plate station.

Habitat Characteristics

The location of each track plate and camera station was recorded using a global positioning system (GPS) unit and basic information on microhabitat characteristics was collected. Slope, aspect, disturbance within a 30 m radius were recorded. Vegetation was described using the California Wildlife Habitat Relationships (CWHR) system to characterize the vegetation community, tree size and canopy closure. We noted the presence, size and decay class of trees and stumps and identified to species where possible. We estimated the relative cover by the dominant tree and shrub species and the proportion of cover area in grass, herbaceous, rock, litter or bare soil. Basal area, tree species composition, decay class and diameters at breast height were collected using variable plot methods using a 20-factor prism and a Biltmore stick. Three 30 m transects were established centered on a location 5 m from the track plate or camera station on a random azimuth to sample coarse woody debris and evidence of anthropogenic disturbance such roads, trails or trash. At the center point and at the transect ends, canopy closure was measured by densiometer.

Explanatory Variables

Explanatory variables were derived from measured or estimated characteristics of microhabitat conditions at each track plate and camera (see above), as well as from GIS data .

GIS-based variables generated for each sample unit center included slope, aspect, elevation, proportion of cover by forest, meadow, shrub, and herbaceous vegetation types, and development at a range of spatial scales (Table 4.1).

Data Analysis

Detection-nondetection data were used to evaluate changes in community composition with development, to model the association of species richness to development and to describe species-habitat associations. The detection of a species at least once by at least one method or at one station (e.g., a single camera, track plate or pellet group plot detection) resulted in a detection for the sample unit. Except where noted, the data used were limited to the detections from the center track plate, camera, and pellet-group plots for all sample units, allowing the incorporation of data from the widest possible array of sample units relative to development level (n=86). A subset of sample units (n=11), typically in areas of high levels of development, were of insufficient size to accommodate the full sample unit array of 4 track plates and 2 camera stations. At these locations, we used a single track plate and camera. The number of pellet-group plots sampled was similarly reduced.

Community Composition and Richness

The relationships between herbivore (rabbits, hares and deer) and carnivore species richness and environmental or development-related variables was described using Poisson regression (PROC GENMOD, SAS Institute 2003) in a model selection framework. We created a suite of a priori models based on explanatory variables grouped by type (e.g. Abiotic, Development Context, Microhabitat structure; see Table 4.1) to capture what we believed to be alternative competing explanations for species distributions and to limit the number of variables in any single model relative to sample size. A full model for each group was evaluated as well as a series of submodels in which a single variable was removed (with replacement) to determine the most influential variable based on a variant of Akaike's Information Criteria (AIC) adjusted for small sample sizes (QAICc). These variables were then assembled into a combined model and allowed to compete with the best models from each group. Finally, variables from each group that were significant at $p< 0.1$ were identified and used to create an additional combined model for evaluation. We identified the most influential variable in the overall best model using the leave-one-out procedure and the change in QAICc value.

Table 4.1. Variables used in regression analyses to evaluate relationships between large mammal richness and occurrence and environmental or development-related variables.

Group	Variable Code	Variable	Source
Anthropogenic	Dev100	% Area developed within 100m radius	GIS, development model
	People	Number of people encountered per hour	Field surveys
	Dogs	Number of dogs encountered per hour	Field surveys
	Vehicles	Number of vehicles encountered per hour	Field surveys
Development Context	Dev300, Dev500, Dev1000,	% Area developed within 300m, 500m or 1000m radius	GIS, development model
	DevMax	Maximum of above values	GIS, development model
Abiotic	Elev	Elevation in meters, average within 100 m area	GIS, digital elevation model
	Slope	Percent slope averaged over 100m area	GIS, digital elevation model
	Ppt_mm	Precipitation, 30 year average in mm	GIS, Daly et al. (2002) statistical mapping of climate
Microhabitat (composition)	Avg_Shrub	Sum of average % cover values for all shrub species	Field measurement
	Avg_Herb	Sum of average % cover values for all herb species	Field measurement
	Avg_Tree	Sum of average % cover values for all tree species	Field measurement
	Total_Cov	Total average % cover of herbs, shrubs, and trees	Field measurement
Microhabitat (structure)	Vol_Cwd	Total volume of coarse woody debris	Field measurement
	Tree_lg	Density of trees, ≥61cm dbh, per ha	Field measurement
	Tree_sm	Density of trees, 12.5-27.9cm dbh, per ha	Field measurement
	Snag_Tot	Density of snags, >30.5cm dbh, per ha	Field measurement

Table 4.1 cont.

Group	Variable Code	Variable	Source
Macrohabitat (composition)	Bar_300, Bar_1K	Percent area within 300 or 1000m classified as Barren	GIS, Dobrowski et al. (2005) vegetation classification crosswalked to CWHR (CDFG 1988) habitat types
	For_300, For1K	Percent area within 300 or 1000m classified as Forest type	
	Mdw_300, Mdw_1K	Percent area within 300 or 1000m classified as Meadow type	
	Shr_300, Shr_1K	Percent area within 300 or 1000m classified as Shrub	
Macrohabitat (structure)	N300_12, N_1K_12	Percent of area within 300 or 1000m distance with trees <15 cm dbh	GIS, Dobrowski et al. (2005) vegetation classification crosswalked to CWHR (CDFG 1988) tree size and density classes
	N34sp_300, N34sp_1K	Percent of area within 300 or 1000m distance with trees 15 – 61 cm dbh and canopy cover < 40%	
	N34md_300, N34md_1K	Percent of area within 300 or 1000m distance with trees 15 – 61 cm dbh and canopy cover ≥ 40%	
	N56sp_300, N56sp_1K	Percent of area within 300 or 1000m distance with trees > 61 cm dbh and canopy cover < 40%	
	N56md_300, N56md_1K	Percent of area within 300 or 1000m distance with trees > 61 cm dbh and canopy cover > 40%	

To examine changes in species composition along the development gradient, we used a non-parametric method to test for differences in composition between sample units grouped by the % development. We used a multi-response permutation procedure with Sorenson's distance measure, a natural weighting factor for each group, and 1000 permutations of group associations (McCune and Grace 2002). The test statistic, T, describes the differences in community composition among sites with 0-1% (n=8), 1-30% (n=38), and > 30% development (n=21). We also evaluated the influence of each species on the differences among development categories by removing a species from the analysis and then replacing it in subsequent analyses. When the change in T, ΔT, is positive, it indicates species whose presence tend to make community composition more different among development categories; a negative value for ΔT indicates species whose presence makes the communities more similar. We also evaluated heterogeneity within development categories using a similarity measure, A, the chance-corrected within-group agreement. When A=0, the within-group heterogeneity equals expectation by chance. As A →1 then sites within the development category are more similar to one another; for A< 0 sites within the development category are more heterogeneous than expected by chance.

Habitat Associations

For carnivore species, logistic regression (PROC NLMIXED, SAS Institute 2003) adjusted for species detectability was used to relate individual species occurrence to explanatory variables describing environmental or anthropogenic conditions (Table 4.1). Models were developed based on local characteristics (such as canopy closure, tree and shrub composition and coarse woody debris), sample unit characteristics (such as composition of habitat types, proportion of adjacent area developed), and matrix characteristics using concentric buffers around the sample unit at varying distances. As described above, we grouped similar variables into groups of models and submodels and evaluated them based on a variant of AIC adjusted for small sample sizes (AICc). We assembled two additional models based on the most influential variables ("best-of-AIC"; the variable in each group effecting the greatest increase in AICc when removed) and those variables that were significant ("best-of-p"; all variables from any group with $p<0.1$).

Activity Patterns

To examine daily activity patterns of carnivores, we used only cameras detections because this is the only method that recorded the time of detection as well as the species detected. We examined daily activity across the development gradient by grouping activity into three periods: dusk to dawn (2000 hours to 0559 hours), dawn to mid-day (0600 to 1259) and mid-day to dusk (1300 to 1959).

Results

Sampling Completed

During June through September 2003 and May through September 2004, 75 sample sites across the development gradient were sampled using the above methods with the full array of track plates, cameras and pellet plot groups. At 11 additional sites, a reduced array of a single track plate, camera and pellet group plots was used. Ten carnivores were detected, eight native species, and the domestic dog and cat, plus the presence of five squirrel species, chipmunks, woodrats and hares and deer (Table 4.2). Results described here focus on the carnivores, leporids and deer detected as these are the species best represented by these methods.

Table 4.2. Species detected in 2003 during track plate, camera, and pellet surveys. Several species are difficult to distinguish and are grouped by genus or family designations.

Scientific name	**Common name**
Martes americana	American marten
Spilogale putoris	Spotted skunk
Mephitis mephitis	Striped skunk
Mustela species	Weasels
Lynx rufus	Bobcat
Ursus americanus	Black bear
Canis latrans	Coyote
Procyon lotor	Raccoon
C. familiaris	Domestic Dog
F. cattus	Domestic Cat
Spermophilis beecheyi	California ground squirrel
S. lateralis	Golden-mantled ground squirrel
Tamaisciurus douglasii	Douglas' squirrel
Glaucomys sabrinus	Northern flying squirrel
Sciurus griseus	Western gray squirrel
Tamias species	Chipmunks
Neotoma species	Woodrats
Leoporid species	Rabbits and hares
Odocoileus hemionus	Black-tailed deer

Domestic dogs were the most commonly detected species at a sample unit and were recorded at 64% of sites (n = 49) (Fig. 4.2). At one sample site, at least 13 distinct individuals were recorded during one, 10-day survey period. Coyote (n = 34), black bear (n = 35), raccoon (*Procyon lotor;* n = 37), and rabbits and hares (Leporid species; n = 45) were each detected at ≥40 % of sample units. The least commonly detected species were bobcat (n = 2), weasels (n = 2), and spotted skunk (n = 3).

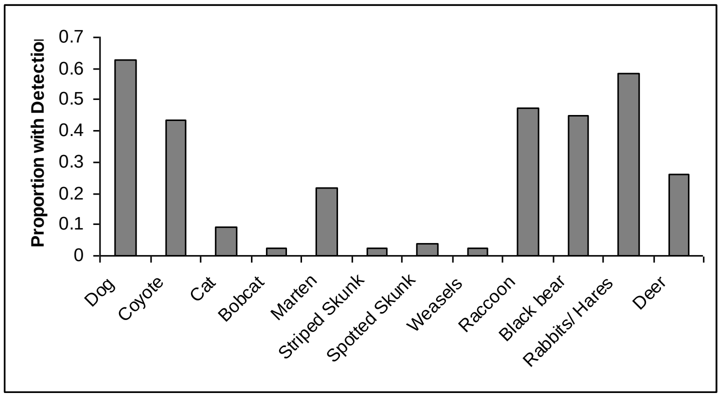


Figure 4.2. Proportion of sample units with at least one detection of the species during track plate, camera or pellet surveys.

Community Composition and Richness

Species richness did not differ significantly along the development gradient (mean = 2.8, s.d. = 1.0; median = 3) and ranged from 1-6 species. Nine sample units recorded 4 native carnivore species. There was some variation in individual species distributions across development classes (Fig. 5 -3). Domestic dogs and raccoons were detected at sample sites across the development gradient, but were somewhat more common at more developed sites. Felids occurred in most development classes. Where the species could be positively identified (e.g.. from a photograph), bobcats accounted for the detections at less developed sites and domestic cats accounted for the detections at more developed sites. Coyotes were relatively evenly distributed across development classes, occurring in approximately 40-60% of sample sites in each development class. Marten and black bear showed a negative response to development with a greater number of detections at less developed sites. Martens dominated detections at the least developed sites (<1 % developed), accounting for 48% of detections, whereas domestic dogs accounted for the majority of detections in all other development categories (Fig. 4.4). Martens and skunks showed a skewed distribution being detected at only those sites where development was < 30% (Fig. 4.5)

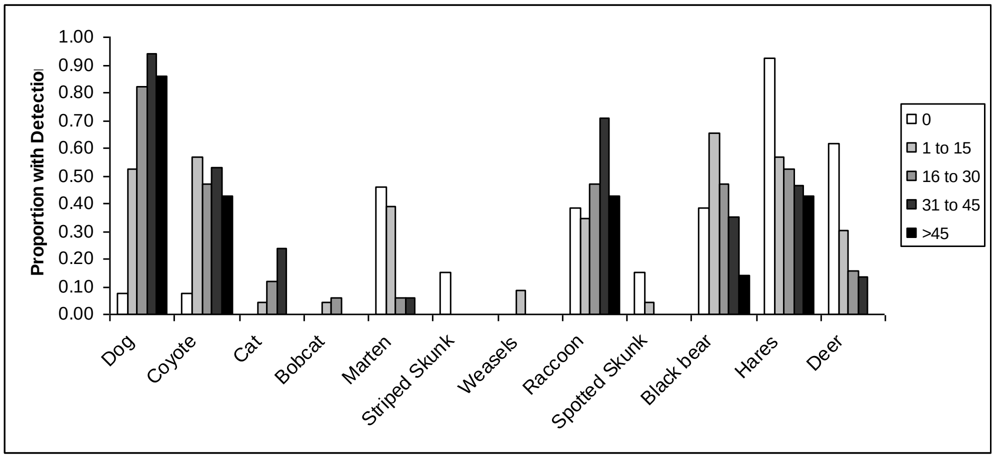


Figure 4.3. Proportion of sample sites in each development class that received at least one detection of the species during track plate, camera or pellet surveys. Development classes refer to the proportion of a 300-m radius circle around the sample unit that was developed.

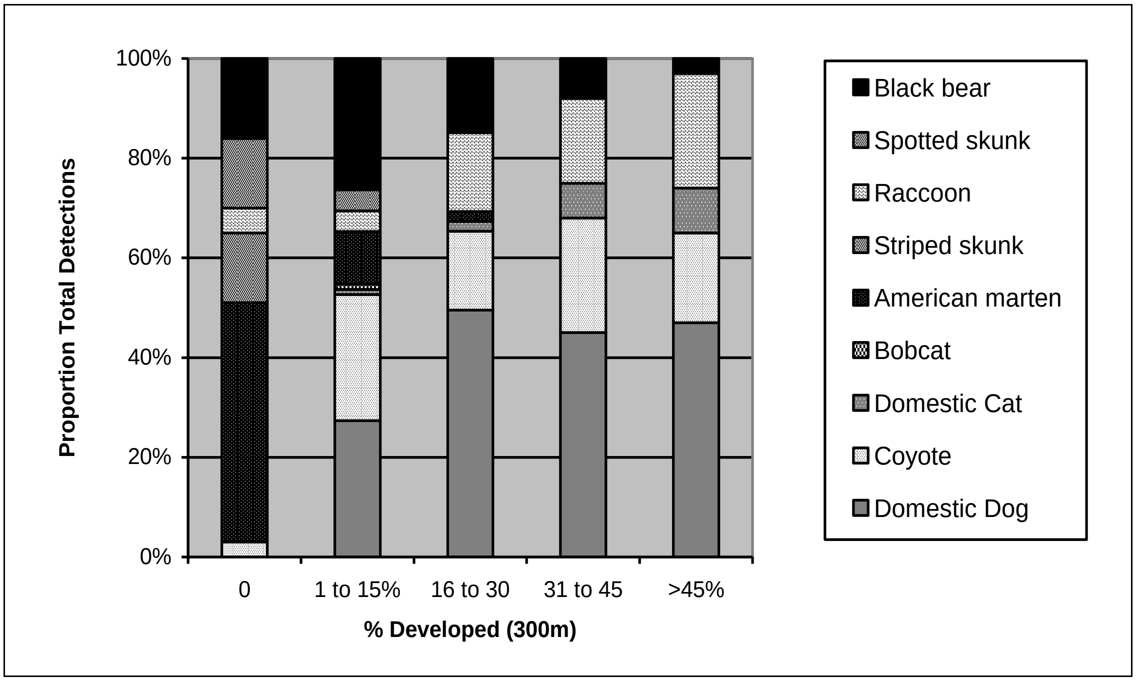


Figure 4.4. Proportion of total detections at track plates and cameras at a sample unit for each species by development category.

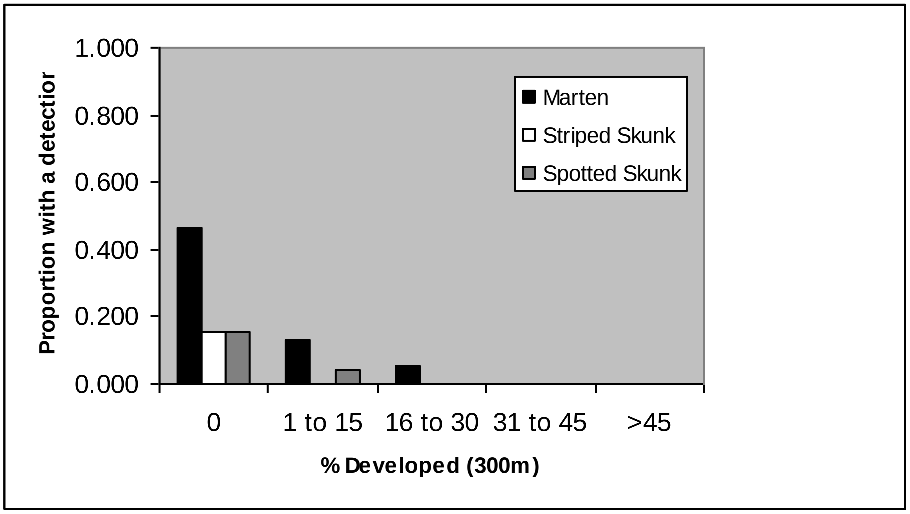


Figure 4.5. Occurrence of mustelids and their allies relative to proportion of a 300m radius circle around the sample unit that was developed.

MRPP analysis indicated significant differences among sites in the three development categories (T=-4.548; p<0.002). Based on multiple comparisons (significant = p < 0.0125), communities at low development sites (<1% developed) were significantly different from communities at high development sites (>30% developed; T=-4.999; p<0.002). Communities at sites with moderate development (1-30% developed) were significantly different from communities at sites with low development ($T=-3.179$; $p<0.011$) but not communities at high development sites ($T=-2.436$; $p<0.030$). Species that had the greatest impact on the observed differences were marten and black bear (Table 4.3). Black bears were fairly broadly distributed along the development gradient (Fig.4.3, 4.4); their presence tended to make communities more similar ($\Delta T>0$) among development categories. In contrast, martens occurred at sites with less development (Fig.4.3, 4.4); their presence tended to make communities more different among development categories ($\Delta T<0$).

Model selection analysis for herbivore species richness identified no single, strong model (best model weight = 28%). The top three models contained variables related to both broad scale macrohabitat and microhabitat structure, as well as anthropogenic influences associated with human development (Table 4.4). For carnivores, species richness was associated with microhabitat characteristics, specifically the volume of coarse woody debris, and the density of large and small trees, as well as the abiotic characteristics of the site (Table 4.5).

Table 4.3. Results of Multi-response permutation procedure analysis of large mammal community composition (7 species at 67 sample units) in the Lake Tahoe Basin 2003-2004. Statistic T reflects the difference in composition among development categories; ΔT is the change in T with the indicated species removed; A is a measure of heterogeneity within development categories. When ΔT is positive, the removed species tends to make the communities more similar when present; when ΔT is negative, the removed species tends to make the communities more different when it is present. All T values were statistically significant (p<0.006) unless noted.

Species removed	**# sites**	***T***	***A***	***ΔT***
All species included	67	-4.548	0.068	
Black bear	62	-6.601	0.108	-1.922
Coyote	61	-4.679	0.077	-0.131
Spotted skunk	67	-4.574	0.070	-0.026
Striped skunk	67	-4.524	0.068	0.024
Weasels	67	-4.491	0.070	0.057
Bobcat	67	-4.410	0.068	0.138
Raccoon	61	-4.113	0.068	0.567
Marten	67	-2.372^{ns}	0.041	2.176

Ns: non-significant

Table 4.4. Performance of models of herbivore richness based on QAICc and Akaike weight. A (-) indicates a negative relationship.

Models	**Variables**	**QAICc**	**Weight**
Macrohabitat (structure) - 1000m	N34sp_1K(-) N34md_1K N56sp_1K N56md_1K	175.201	0.2813
Microhabitat (structure)	Vol_Cwd Tree_lg(-) Tree_sm(-)	176.039	0.1863
Anthropogenic	Dev_100m(-) People Vehic(-)	176.338	0.1604
Macrohabitat (composition) – 300m	For_300 Mdw_300* Shr_300	176.419	0.1541
Macrohabitat (structure) – 300m	N300_12(-) N34sp_300(-) N34md_300(-) N56sp_300(-)	176.473	0.1499
Macrohabitat (composition) – 1000m	Bar_1K For_1K Shr_1K(-)	179.044	0.0415
Development context	Dev_300m Dev_500m Dev_1000m(-)	181.174	0.0143
Abiotic	Elev Ppt_mm(-)	181.935	0.0098
Microhabitat (composition)	Avg_Shrub Avg_Herb(-) Avg_Tree Total_Cov	187.546	0.0006
Best of p<0.1	Dev_100m(-) Dogs(-) Slope Snag_Tot Avg_Shrub Avg_Herb(-) Mdw_1K(-) Shr_1K(-)	182.684	0.0000

Table 4.5. Performance of models of carnivore richness based on QAICc and Akaike weights. A (-) indicates a negative relationship.

Models	Variables	QAICc	Weight
Microhabitat (structure)	Vol_Cwd Tree_lg Tree_sm*(-)	226.270	0.4828
Abiotic	Ppt_mm*(-) Slope	226.976	0.3392
Anthropogenic	Dev_100m(-) People(-) Dogs	229.743	0.0850
Microhabitat (composition)	Avg_Shrub(-) Avg_Herb(-) Avg_Tree Total_Cov	230.465	0.0593
Development context	Dev_300m Dev_500m(-) Dev_1000m	232.814	0.0183
Macrohabitat (composition) – 300m	Bar_300 Mdw_300 Shr_300(-)	234.037	0.0099
Macrohabitat (structure) – 300m	N300_12(-) N34sp_300(-) N56sp_300(-) N56md_300(-)	235.706	0.0043
Best of AIC	Dogs Slope Tree_sm Shr_300(-) N34sp_1K(-) N56md_1K(-)	239.659	0.0006
Macrohabitat (composition) – 1000m	N_1K_12(-) N34SP_1K(-) N56SP_1K(-) N56MD_1K(-)	240.581	0.0004
Macrohabitat (structure) – 1000m	Bar_1K(-) Mdw_1K(-) Shr_1K(-)	241.919	0.0002
Best of p<0.1	Dev_Max(-) Elev(-) Snag_Tot For_300 N300_12 N34sap_300 N34md_300 N56md_300	255.326	0.0000

*Most influential variable based on QAICc

Habitat Associations

Species differed in the suites of variables most strongly associated with their occurrence. For rabbits/hares, abiotic characteristics of the site were most strongly associated with occurrence (weight = 22%) followed by microhabitat structure, anthropogenic characteristics and macrohabitat composition (Table 4.6a). The occurrence of deer was strongly associated with a combined model consisting of development and human disturbance-related variables, slope and microhabitat structure (weight = 99%; Table 4.6b).

Table 4.6. Performance of models of herbivore occurrence based on AICc and Akaike weights. A (-) indicates a negative relationship.

a) Rabbits/hares

Models	Variables	AICc	Weight
Abiotic	Elev Ppt(-) Slope	92.750	0.2220
Microhab. structure	Vol_Cwd(-) Tree_lg(-) Tree_sm Snag_tot	94.063	0.1151
Anthropogenic	Dev_100m(-) People Dogs(-) Vehic(-)	94.063	0.1151
Macro 300 composition	Bar_300(-) For_300 Mdw_300 Shr_300	94.063	0.1151
Macro1000 composition	Bar_1K For_1K Mdw_1K(-) Shr_1K(-)	94.063	0.1151
Develop. context 1	Dev_300m Dev_500m(-) Dev_1000m Dev_Max(-)	94.063	0.1151
Macro 1000 structure	N_1K_12(-) N34sp_1K(-) N34md_1K(-) N56sp_1K(-) N56md_1K(-)	95.436	0.0580
Macro 300 structure	N300_12 N34sp_300 N34md_300 N56sp_300	95.436	0.0580
Microhab. composition	Avg_Shrub Avg_Herb Avg_Tree Total_Cov	95.436	0.0580
Best of p<0.1	Dogs(-) Snag_Tot Avg_Herb(-) For_300(-) Bar_1K Shr_1K(-)	96.870	0.0283

b) Deer

Models	Variables	AICc	Weight
Best of P<0.1	People Dogs(-) Dev_300m Dev_max(-) Slope Avg_Shrub Vol_Cwd	38.2494	0.9995
Abiotic	Ppt_mm(-) Slope	54.8884	0.0002
Best of AIC	Dogs(-) Slope Vol_Cwd Tree_lg(-) Mdw_1K(-)	56.3276	0.0001
Anthropogenic	Dev_100m(-) People Dogs(-)	56.9664	0.0001
Development context 1	Dev_300m Dev_500m Dev_Max(-)	59.2288	0.0001
Macrohab comp 1000m	Bar_1K(-) For_1K(-) Mdw_1K(-)	61.5885	0.0000
Microhab struct	Vol_Cwd Tree_lg(-) Snag_Tot	62.4139	0.0000
Macrohab struct 1000m	N_1K_12 N34sp_1K N34md_1K N56sp_1K	68.3052	0.0000
Macrohab struct 300m	N300_12(-) N34sp_300(-) N34md_300(-) N56md_300(-)	68.8208	0.0000

Predictably, the non-native species, domestic dog and cat, were strongly associated with anthropogenic influences. Four of the top five models for domestic dog and three of the top five models for domestic cat contained variables describing development or anthropogenic site characteristics (Table 4.7a, b). The best model for domestic dog was based on development context (weight = 78%). Models containing development and anthropogenic characteristics also performed well to describe the occurrence of two native species considered to be tolerant of human presence and activity: coyote and raccoon. Three of the top four models for coyote occurrence contain variables associated with anthropogenic influences (Table 4.8a). Coyote occurrence was associated with development within 100m, human activity, vehicles, and abiotic site characteristics. The best model of coyote occurrence was based on anthropogenic influences (weight = 54%). Raccoons were associated with development at multiple spatial scales, dogs, microhabitat structure and macrohabitat composition (weight = 40%; Table 4.8b).

Two native species were less strongly associated with anthropogenic influences: marten and black bear. For these species, models with environmental or habitat variables tended to perform better than those with development or anthropogenic variables only. When development or anthropogenic variables did occur in top models, the relationship was generally a negative one. The best model for marten occurrence was a combined model human activity and total snag density (weight = 48%). The second best model for marten was based on macrohabitat composition (weight = 43%; Table 4.9a). Models based on development context (weight = 2%) and anthropogenic influences (weight = 0.05%) performed poorly for marten occurrence (Table 4.9a). The best model for black bear occurrence was comprised of macrohabitat composition variables. The next best model for black bear was based on a negative relationship between bear occurrence and development, human activity and vehicles (Table 4.9b).

Table 4.7. Performance of models of domestic dog and cat occurrence based on AICc and Akaike weights. (-) indicates a negative relationship.

a) Domestic dog

Models	**Variables**	**AICc**	**Weight**
Development context	Dev_300m(-) Dev_1000m(-) Dev_Max*	400.129	0.7828
Best of AIC	Dev_100m(-) Dev_Max Elev(-) For_1K	404.510	0.0876
Best of p<0.1	Dev_100m(-) Dogs Dev_Max Dev_1000m(-) Elev(-) Avg_Shrub(-) Avg_Herb Snag_Tot Bar_300 For_1K	404.549	0.0859
Anthropogenic	Dev_100m People Dogs	406.580	0.0311
Abiotic	Elev(-) Slope	408.416	0.0124
Macrohabitat (structure) – 1000m	N34sp_1K(-) N34md_1K(-) N56sp_1K(-) N56md_1K(-)	417.145	0.0002
Macrohabitat (composition) – 1000m	Bar_1K(-) For_1K(-) Mdw_1K	418.459	0.0001
Macrohabitat (composition) – 300m	Bar_300 For_300(-) Mdw_300	421.684	0.0000
Macrohabitat (structure) – 300m	N300_12(-) N34sp_300(-) N34md_300(-) N56md_300(-)	421.684	0.0000
Microhabitat (composition)	Avg_Shrub(-) Avg_Herb Avg_Tree(-)	424.511	0.0000
Microhabitat (structure)	Tree_lg(-) Tree_sm Snag_Tot(-)	425.551	0.0000

*Most influential variable based on AICc

b) Domestic cat

Models	**Variables**	**AICc**	**Weight**
Best of p<0.1	Avg_Herb	107.521	0.2171
Best of AIC	Dev_100m	108.034	0.1680
Anthropogenic	Dev_100m People Vehic(-)	108.567	0.1287
Abiotic	Slope(-) Elev(-)	108.643	0.1239
Development context	Dev_300m Dev_500m(-) Dev_Max	108.834	0.1126
Microhabitat (structure)	Vol_Cwd(-) Tree_lg(-) Snag_Tot	109.175	0.0949
Microhabitat (composition)	Avg_Shrub(-) Avg_Tree(-) Total_Cov	110.002	0.0628
Macrohabitat (composition) – 300m	Bar_300(-) For_300(-) Mdw_300	111.854	0.0249
Macrohabitat (composition) – 1000m	For_1K(-) Mdw_1K(-) Shr_1K(-)	114.545	0.0065
Macrohabitat (structure) – 300m	N34sp_300 N34md_300(-) N56sp_300(-) N56md_300(-)	114.741	0.0059
Macrohabitat (structure) – 1000m	N34sp_1K N34md_1K(-) N56sp_1K(-) N56md_1K(-)	117.764	0.0013

*Most influential variable based on AICc

Table 4.8. Performance of models of coyote and raccoon occurrence based on AICc and Akaike weights. (-) indicates a negative relationship.

a) Coyote

Models	Variables	AICc	Weight
Anthropogenic	Dev_100m People* Vehic(-)	323.936	0.5405
Best of AIC	Vehic(-)	327.732	0.0824
Best of p<0.1	Vehic(-) Avg_Shrub(-)	328.015	0.0715
Abiotic	Elev(-) Ppt_mm(-)	328.062	0.0699
Microhabitat (composition)	Avg_Shrub(-) Avg_Tree(-) Total_Cov	329.388	0.0360
Macrohabitat (composition) – 300m	Bar_300 For_300(-) Shr_300(-)	330.536	0.0203
Macrohabitat (structure) – 300m	N300_12 N34sp_300 N34md_300 N56sp_300	330.678	0.0189
Macrohabitat (composition) – 1000m	Bar_1K(-) For_1K(-) Mdw_1K	330.753	0.0182
Development context	Dev_300m Dev_1000m Dev_Max(-)	331.460	0.0128
Microhabitat (structure)	Vol_Cwd(-) Tree_lg(-) Tree_sm(-) Snag_Tot(-)	332.229	0.0095
Macrohabitat (structure) – 1000m	N34sp_1K(-) N34md_1K(-) N56sp_1K N56md_1K(-)	334.299	0.0032

*Most influential variable based on AICc

b) Raccoon

Models	Variables	AICc	Weight
Best of p<0.1	Dogs Dev_300m Dev_500m(-) Dev_1000m Avg_tree Shr_1K*(-)	221.869	0.4039
Macrohabitat (composition) – 1000m	Bar_1K(-) Mdw_1K Shr_1K(-)	222.694	0.2674
Anthropogenic	Dev_100m People Dogs(-)	225.445	0.0676
Best of AIC	Dogs Dev_300m Tree_lg	226.354	0.0429
Development context	Dev_300m Dev_500m(-) Dev_1000 Dev_Max(-)	227.097	0.0296
Macrohabitat (composition) – 300m	Bar_300(-) Mdw_300 Shr_300(-)	227.353	0.0260
Abiotic	Elev Slope(-)	227.586	0.0232
Microhabitat (composition)	Avg_Shrub Avg_Tree Total_Cov(-)	227.635	0.0226
Microhabitat (structure)	Vol_Cwd(-) Tree_sm Tree_lg	228.351	0.0158
Macrohabitat (structure) – 1000m	N34sp_1K(-) N34md_1K N56sp(-)_1K N56md_1K	228.899	0.0120
Macrohabitat (structure) – 300m	N34sp_300 N34md_300 N56sp_300 N56md_300	229.843	0.0072

*Most influential variable based on AICc

Table 4.9. Performance of models of marten and black bear occurrence based on AICc and Akaike weights. (-) indicates a negative relationship.

a) Marten

Models	Variables	AICc	Weight
Best of AIC	People(-) Snag_Tot*	96.307	0.4769
Macrohabitat (composition) – 1000m	For_1K Mdw_1K Shr_1K(-)	96.515	0.4299
Macrohabitat (structure) – 1000m	N34SP_1K N34MD_1K N56SP_1K N56MD_1K	101.641	0.0331
Best of p<0.1	Dev_500m Elev Avg_Herb Avg_Tree Total_Cov	102.633	0.0202
Development context	Dev_300m(-) Dev_500m(-) Dev_1000m	102.750	0.0190
Microhabitat (structure)	Tree_sm(-) Tree_lg(-) Snag_Tot Total_Cov(-)	103.952	0.0104
Abiotic	Elev Ppt_mm(-)	104.676	0.0073
Macrohabitat (composition) – 300m	For_300 Mdw_300 Shr_300	107.069	0.0022
Anthropogenic	Dev_100m(-) People(-) Dogs(-)	110.259	0.0005
Macrohabitat (structure) – 300m	N_300_12 N34sp_300 N34md_300 N56md_300	110.410	0.0004
Microhabitat (composition)	Avg_Herb Avg_Tree Total_Cov	112.614	0.0000

*Most influential variable based on AICc

b) Black bear

Models	Variables	AICc	Weight
Macrohabitat (composition) – 300m	Bar_300 For_300* Shr_300	251.018	0.3233
Anthropogenic	Dev_100m(-) People(-) Vehic(-)	251.728	0.2267
Best of p<0.1	Bar_300 For_300* For_1K N34md_1K	252.044	0.1936
Macrohabitat (structure) – 300m	N300_12(-) N34sp_300(-) N34md_300(-) N56sp_300(-)	253.427	0.0969
Macrohabitat (composition) – 1000m	Bar_1K(-) For_1K Shr_1K	253.657	0.0864
Best of AIC	Snag_Tot For_1K N56md_1K	255.412	0.0359
Development context	Dev_300m(-) Dev_1000m Dev_ Max(-)	258.253	0.0087
Microhabitat (structure)	Tree_sm(-) Tree_lg(-) Snag_Tot	258.277	0.0086
Macrohabitat (structure) – 1000m	N34sp_1K N34md_1K N56sp_1K N56md_1K	259.141	0.0056
Abiotic	Elev Ppt_mm(-)	259.449	0.0048
Microhabitat (composition)	Avg_Shrub Avg_Tree Total_Cov(-)	262.156	0.0012

*Most influential variable based on AICc

Activity Patterns

Species varied in the time of day during which they were detected most frequently. Dogs were generally detected during daylight hours; in contrast, coyotes were generally detected after dusk (after 2000 hours) and before dawn (before 0600 hours; Fig. 4.6 and 4.7). Of note is the tendency toward coyote detections during the day as well as at night at the less developed sample units.

Black bear exhibited strong nocturnal behavior at sample units with moderate to high levels of development, whereas bears were active during all time periods at less developed sites (Fig. 4.7). Coyotes appeared to be active primarily a night across the development gradient with some activity during the day at low to moderately developed sites. Raccoons were active primarily at night but indicated a trend to greater activity during daylight hours at more developed sites.

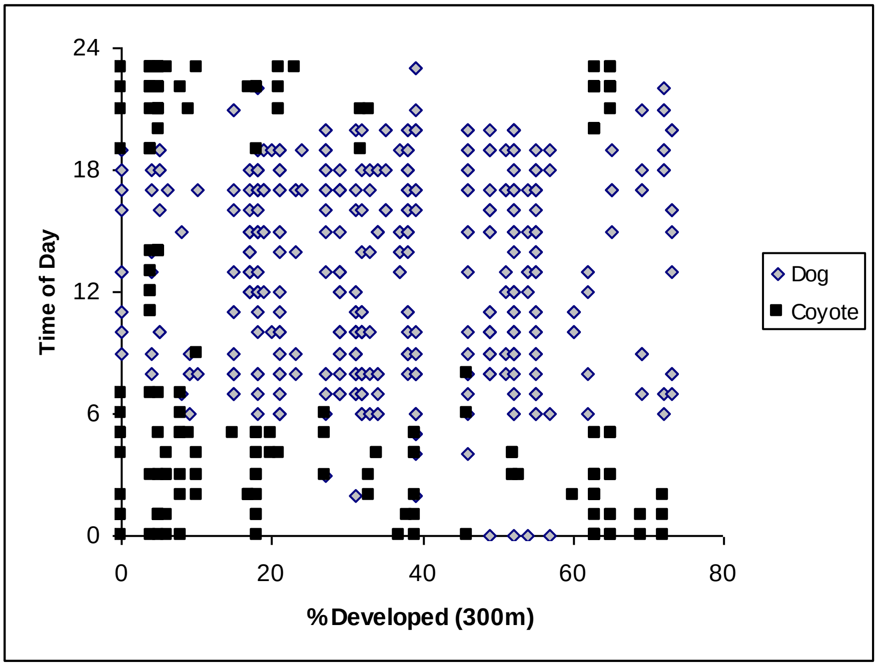


Figure 4.6. The temporal distribution of camera detections of dogs and coyotes relative to the development gradient.

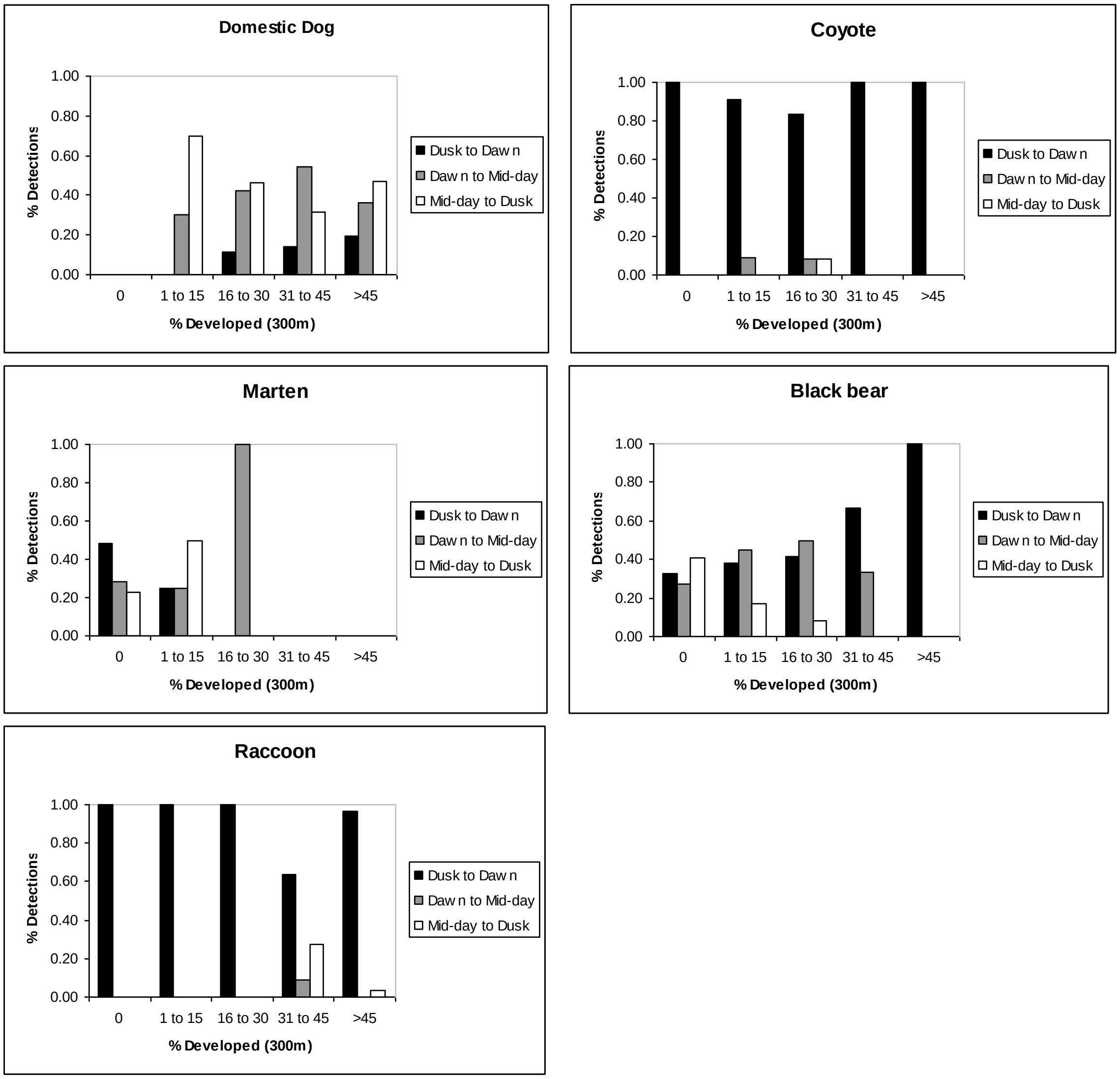


Figure 4.7. Temporal distribution of carnivore activity across the development gradient. Time periods are: dusk to dawn (2000 hours to 0559 hours), dawn to mid-day (0600 to 1259) and mid-day to dusk (1300 to 1959).

Discussion

Composition of the carnivore community was affected by development and human disturbance through the composite of positive and negative responses of individual species. Richness is not a sensitive measure of community change, given the small number of species comprising the carnivore community and the compensatory responses observed among the carnivore species, where just as many species appeared to be positively affected by development as were negatively affected. Changes in composition were a more effective means of detecting community-wide responses to development. Marten and raccoon, representing negative and positive responders, respectively, appeared to have the greatest effect on composition along the development gradient. Marten is among the top mammalian predators in Lake Tahoe, and their absence in more developed areas could affect the abundance of their prey (primarily voles, chipmunks and squirrels). Raccoon is an omnivore, their greater occurrence in more developed areas is unlikely to have a substantive effect on trophic dynamics.

Species are expected to vary in their response to development and human active given differences in species morphology and life history characteristics (Crooks 2002, Gehring and Swihart 2003). Species that can utilize a broad array of resources may be less sensitive to development and consequently more tolerant of a heterogeneous environment (Bright 1993). The occurrence and activity of raccoons and coyotes, as well as the occurrence of dogs and cats, were neutrally or positively associated with human development and activity. Generalist species may be neutrally or positively affected by habitat modification, and are more likely to be relatively tolerant to both development and anthropogenic disturbance. An extreme example of this would be species such as raccoons, squirrels, and crows which can live commensally with humans and take advantage of anthropogenic features and food sources. In contrast, the occurrence of marten (a habitat specialist) and, to a lesser extent, black bear were negatively associated with increasing levels of development and human activity.

The generally poor performance of models of herbivore richness may be attributable to this study's bias toward forested sample units and to the emphasis placed on describing forest characteristics in model development. Variables related to microhabitat structure provided the best model for carnivore species richness followed by intrinsic, abiotic site characteristics. Deer and rabbits/hares were more frequently detected at less developed sites which may reflect the higher levels of associated ground disturbance with development, reduced forage availability, and the presence of dogs.

Overall, development was a greater influence than human activity on species occurrence and relative activity levels. However, species most sensitive to development also exhibited alterations in their temporal patterns of habitat use. Based on the timing of detections, coyotes and black bears in the Lake Tahoe Basin appeared to be active throughout the day at less developed sample units but primarily were nocturnal at more developed sample units. This shift in activity pattern would tend to minimize activity during the time periods with the greatest activity by humans and domestic dogs. In contrast, raccoons exhibited a trend toward more broad activity periods in areas of greater development, becoming increasingly active in during daylight hours. This shift in activity may represent tolerance of human activity. Such shifts in activity pattern may be benign or may result in reduced time spent on foraging or reproductive activities (Knight and Gutzwiller 1995, Frid and Dill 2002). Determining the conservation importance of these activity shifts would require a more focused study of the behavior of the species concerned (Gill et al. 2001).

The nearly ubiquitous presence of dogs has great ecological significance. Although somewhat less frequently detected at less developed sample units, dogs were detected across the development gradient and the majority were off-leash. That at least 13 individuals were detected multiple times during a single ten-day period suggests the effect that domestic dogs could have on local wildlife and highlights the need for further investigation of their possible impacts.

The responses we observed during the summer may not be consistent with winter use. Sample units surrounded by higher levels of development appeared to provide some habitat for species tolerant of an anthropogenic environment. Information on the use of developed areas during the winter, when patterns of both human and dog activity may be different might be informative. Species that do not use more developed areas in the summer when human activities may be more dispersed, may be able to utilize some areas during the winter when activity is more likely to be concentrated at developed recreation areas such as ski resorts and snow parks. Since winter is a more energetically stressful period for some species of wildlife, the use of more developed areas during winter could represent an important function of these areas. Information on seasonal shifts in occurrence patterns along the development gradient could help separate the relative importance of development and human activity, and could help clarify the importance of more developed areas for wildlife.

These analyses were based on detection devices located at the center of forested sample units. Consequently these results best represent use of native vegetation with varying levels of insulation from development. For species sensitive to human activity or development, the availability, abundance and, potentially, the configuration, of native vegetation presumably determines whether these species can use an area in proximity to development. In the absence of remnant native vegetation, some species, such as black bear and marten, might not be found in proximity to even low or moderate development. Urban forest likely plays an important role in maintaining the distribution and abundance of carnivores in the lower elevation areas of the LakeTahoe basin. Future analyses will examine the influence of the amount and configuration of native forest surrounding each sample unit on species occurrence.

Chapter 5:
Ants

Introduction

Many terrestrial arthropods are sensitive to environmental impacts such as fragmentation, disturbance, habitat modification, ecological disruption, climate change, and chemical pollution. Effective indicator taxa can provide a pre-warning of ecological consequences caused by fragmentation – this attribute alone makes arthropods an important basis for scientifically based reserve design and management (Kremen et al. 1993). Ants provide an ideal indicator group for ecological monitoring and assessing environmental impacts (Kaspari and Majer 2000), as they possess numerous attributes ideal for biodiversity studies. These attributes include high diversity and numerical dominance in nearly every habitat worldwide (Agosti et al. 1994, Agosti et al. 2000), readily identified (Brown 2000), easily collected, sensitive to environmental change (Anderson 2000), and they have important functions in ecosystems, including important interactions with organisms from all trophic levels and themselves occupying all trophic levels (Hölldobler and Wilson 1990, Kaspari 2000, Schultz and McGlynn 2000).

Methods

Sample Sites

We selected 124 core sample sites to represent an urban development gradient in the basin. Since the primary sampling frame focused on larger scale effects of disturbances such as development, we additionally assessed the effects on diversity at a smaller scale. We also assessed the effects of particular types of ground disturbances on ant diversity by measuring richness and abundance at increasing distances away from three disturbance types: highway, OHV trail, and residential areas. We sampled multiple types of disturbances within a single large area. Sites meeting appropriate conditions for the distance from disturbance study were quite limited, so we selected one large area where we could fit three replicates per disturbance type. Within each of these 'site replicates' we placed five traps (distance replicates) along transects at 0, 10, 20, 50, 100, and 200 meters from each disturbance type.

Pitfall Trapping

The sampling design targeted ground-dwelling ants since most species constitute this category rather than tree, shrub, or herb-dwelling species. Quantitative data on species distributions were obtained from standard pitfall trapping methods because it is rapid, repeatable, quantitative, and provides a relatively unbiased sample of ants within an area (Anderson 1990, Agosti et al. 2000). Pitfall traps consisted of 6.5-cm diameter (120 ml) plastic cups. This size of trap was appropriate for sampling ants because traps of a 42-mm diameter have demonstrated the same efficacy as traps of varying diameters (Bestelmeyer et al. 2000). Traps were left open for seven days containing approximately 25 ml of propylene glycol. We used propylene glycol as a standard preservative for ant sampling because it does not differentially attract or repel ants, it is nontoxic to vertebrates, and it kills specimens quickly to prevent specimens from destroying each other (Bestelmeyer et al. 2000).

To assess differences between sites according to the large scale primary sampling frame, we used a 40 x 40-m grid to establish 12 pitfall traps per site. Four traps each were placed along three 40-m transects oriented north-south and centered on the center point in each plot (Fig. 5.1a). Transects were separated by 20 m. We used systematic random placement of traps along each transect, whereby the first trap was randomly placed along the first 10 m of each transect and each following trap was staggered at 10-m intervals (Anderson 1997). We marked each trap with a pinflag 1 m north of the trap to avoid direct attraction or damage to traps by other animals.

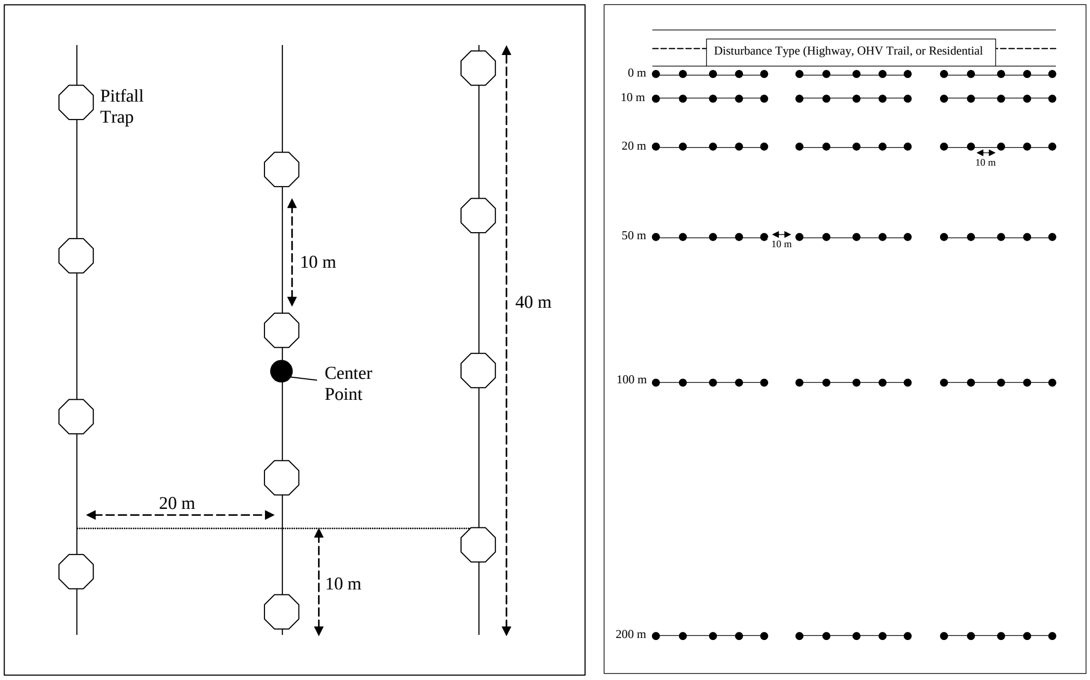


Figure 5.1. Ant pitfall trapping arrays for (a) the large-scale primary sampling frame and (b) the small-scale disturbance type-distance sampling frame. Distances on graphics are not to scale.

In addition to site condition data provided by vegetation measurements (see plant section below), we ranked sample site disturbance within our sampling grids at 72 sites in 2003. We defined disturbance to be any form anthropogenic modification of the site and it consisted of recreational use, forest thinning, burning, or trash buildup. We ranked sites as follows: 0 = none to low disturbance - unaffected by recent human land use or had little evidence of vegetation or soil disturbance, with no more than 10% of the site disturbed; 1 = moderate disturbance – vegetation and ground surfaces were noticeably disturbed, with 10 to 50% of the site having evidence of disturbance; and 2 = high disturbance – sites highly modified by human land use practices, with more than 50% of the area appearing disturbed.

A second trapping array was used to assess ant responses to small scale disturbances. We established a trapping array with three replicates per site at distance intervals of 0, 10, 20, 50, 100, and 200 m from the disturbance extending into wildlands (Fig. 5.1b). At each distance interval, we established a line of five traps spaced 10 m apart and running parallel to the disturbance. We attempted to minimize variation in our samples by minimizing site variability:

we selected sites only in the southern part of the basin; selected sites of similar physiognomy; and selected sites where sampling transects ran toward wildlands and not other types of disturbances (e.g., OHV, residential, commercial, roads).

Pitfall trap samples were sorted to species in our laboratory at University of Nevada, Reno. Species abundances were scored (transformed to ordinal scale data) according to standard methods using a 6-point scale (Anderson 1997): 1 = 1, 2 = 2-5 ants, 3 = 6-10 ants, 4 = 11-20 ants, 5 = 21-50 ants, and 6 = >50 ants. This scaling transformation minimizes distortions caused by large numbers of individuals falling into small numbers of traps due to placement near nests and/or foraging trails.

Data Analysis

We conducted analyses (using SYSTAT v. 10) at the individual, functional group, and full community level. For these analyses we calculated species richness (SR) as total species per site and as mean species per trap. Abundance was calculated as the sum of abundance scores at individual traps and was often expressed as a percentage of its maximum (i.e. maximum of 72 for an individual species). We grouped ants into functional guilds that represented body size, nesting strategies, distributional patterns. Body size was measured as the mean length of ants measured in mm. Nesting strategies were identified as ground, stone, logs, and thatch according to P.S. Ward (personal communication). I categorized each species' nesting strategies as 1=uses only one nest strategy, 2=uses 2 nesting strategies, and 3=uses 3 nesting strategies. We used elevational range as a proxy for individual species distribution. Elevation range was determined using collection data from Wheeler and Wheeler (1986) and synthesized in M. P. Sanford (unpublished data).

We constructed a species-accumulation curve and point versus site richness curve to assess the ability of our sampling grids to detect species within sites. Species-accumulation curves are often used to identify how well a trapping array worked to detect all or most species within a site. Point versus site species richness curves should indicate the turnover of species between traps (Anderson 1997).

We constructed dominance-diversity curves (May 1975) to examine community evenness over all sites combined and to compare community evenness between high and low development sites. We fitted a linear regression model of logarithmic species abundance against arithmetic species rank order for high, moderate, and low development (Bazzaz 1975, Tokeshi 1993). Using the 100-m scale of percent development, sites were grouped as follows: low = 0, moderate = 0.1 – 30, high > 30%. The regression slope of zero indicates a community where all species have equal abundance, whereas greater slopes (i.e., more negative or more positive slopes) indicate greater dominance of a species subset.

We examined community, guild, and individual-level responses in relation to percent development at varying scales. First, we examined the response of species richness and abundance for all sites over six different scales of development. Second, we assessed patterns of guild responses to development at the 100-m scale by examining scatter plots. Third, we examined how individual species changed in abundance with increasing development at the 100-m scale.

Ant responses to finer-scale disturbances were assessed using two procedures. First, we examined responses of species richness and abundance across site-specific disturbance categories using a one-way ANOVA for each response variable. Second, the effect of disturbance type (i.e., highway) and distance from disturbances was evaluated using a two-way ANOVA. To date, we have processed and analyzed ant diversity from the subsample of 0, 50, 100 m distances.

Under the premise that urbanization leads to recreational use within urban lots, we assessed the potential effects of human recreational use on ant communities. We used simple regression analyses to explore responses of ant richness and abundance against six potential explanatory variables of human recreational use: human detections, dog detections, area of compacted ground, area of trails, area of roads, and total compacted surface. Total area of compacted surface is different from area of compacted ground and was calculated by summing areas of compacted ground, trails, and roads within our sites.

To further understand potential site-specific factors that may be driving changes in ant communities, we examined ant responses to three vegetation characteristics that may result (directly or indirectly) from urbanization. We examined coarse woody debris (CWD), impervious surface, and tree density. Pearson correlation coefficients were used to test whether these factors may cause changes in ant richness, abundance, and guild composition.

Results

From the primary sampling framework, 101 sites were sampled over the course of two years in 2003 and 2004. We attempted to provide an even distribution of sample sites around the basin, but east and west sides were limited in the high disturbance categories. Thus, our 2004 samples were largely concentrated on the north and south sides of the basin where site physiognomy was similar.

Large-scale Patterns of Diversity and Dominance

A total of 32,023 individuals from 46 species (Appendix 5.1) were recorded from the 101 sites along the urban disturbance gradient. The richest subfamilies were Formicinae (30 species) and Myrmicinae (13 species). The most common species recorded were *Formica sibylla*, *Formica obscuripes*, *Formica aserva*, and *Camponotus modoc*. *Stennema smithi*, *Tetramorium caespitum*, and *Myrmecocystus testaceus* (a hot climate species) were the least common species detected. Site species richness ranged from 3 to 20 species, and a species-accumulation curve indicated that a large majority of species were captured at each site (Fig. 5.2). Site species richness and point species richness were significantly correlated (Fig. 5.3; $r = 0.45$, $P < 0.001$), indicating a predictable pattern of turnover between traps. This also explains why abundance was a relatively strong predictor of species richness ($r = 0.60$, $P < 0.0001$).

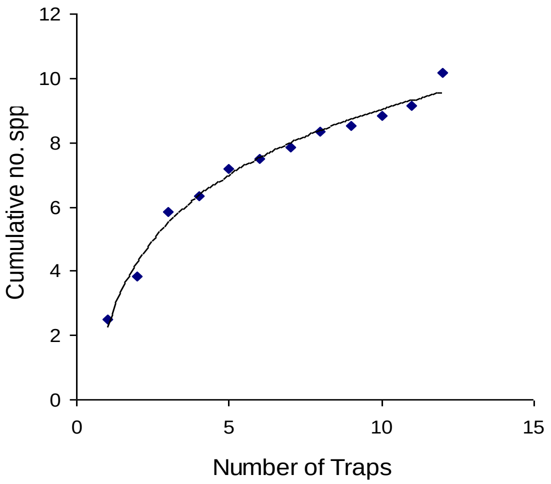


Figure 5.2. Accumulation of ant species in pitfall traps (12 traps per site) averaged over all sites.

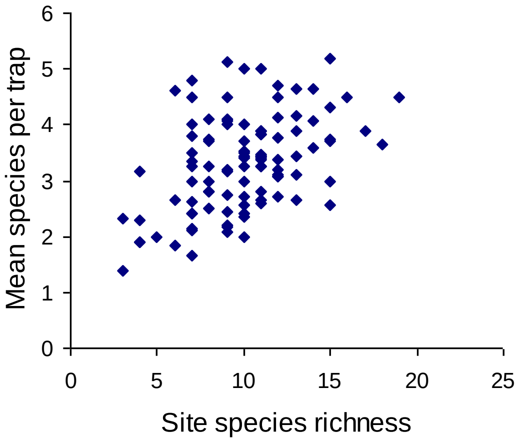


Figure 5.3. Pattern of site species richness (total number of species per site) and point species richness (mean number of species per pitfall trap) along the development gradient.

Species rank-abundance plots demonstrated that ant communities in all development classes were consistent with the broken-stick community model: low sites ($X^2 = 44.5$, $df = 9$, $p < 0.001$); moderate sites ($X^2 = 370$, $df = 11$, $p < 0.001$); high sites ($X^2 = 90$, $df = 10$, $p < 0.001$). Low development sites had a progressively steeper slope as more species were added to the community than did high development sites (Fig. 5.4), indicating that dominance was greater in high development areas. In high development sites, dominance by *Formica sibylla* was 67.0% to 99.9% greater than any other species, whereas the most dominant species exceeded any other species' abundance by only 6.1% in moderate sites and 1.4% in low development sites.

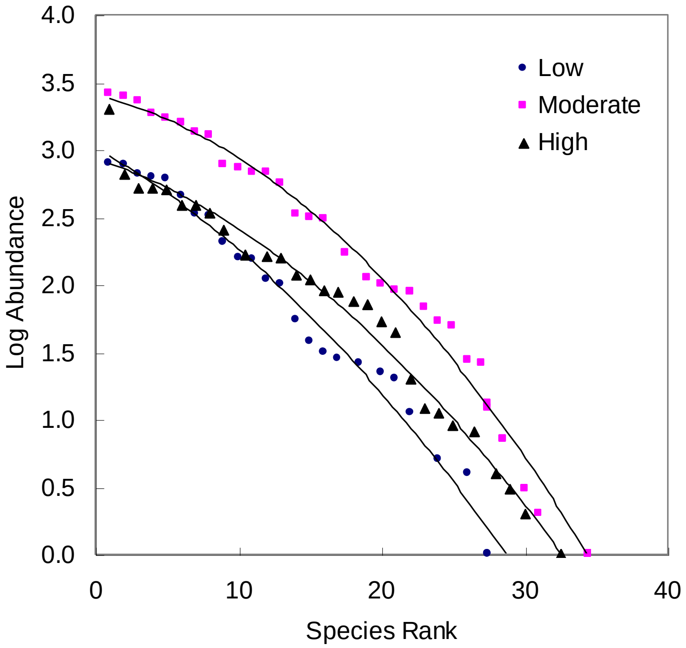


Figure 5.4. Dominance-diversity curve for ant species in the Lake Tahoe basin grouped into urban development categories.

Species richness was not significantly correlated with percent development at the 30 and 60-m scales (*P* > 0.427; Fig. 5.5). At the 100-m scale, a nonlinear model fit where species richness peaked at intermediate levels of development – around 30% developed (*P* < 0.05). Species richness increased across the gradient at the 300-m (*P* = 0.06), 500-m (*P* = 0.02), and 1000-m (*P* = 0.03) scales.

Ant total abundance was not significantly correlated with percent development at any scale (*P* > 0.19 in all cases; Fig. 5.6). However, total abundance showed a decline in the maximum abundance by approximately one-third as landscape development (300, 500, and 1000 m) increased. The proportion of sites with different levels of total ant abundance differed substantially between low (< 20%) and high (≥ 20%) development sites (Fig. 5.7), with low development sites having

Ant species were divided into four functional groups and we found that species abundance as specialist ground nesters (Fig. 5.8a), mean elevational range of species (Fig. 5.8c), mean body length of species (Fig. 5.8d) did not differ across the development gradient (*P* >0.05 in all cases). The abundance of species specializing as log nesters demonstrated no significant declines (*P* = 0.19) with development, but the pattern suggests interactions between habitat and log nesting ants across the development gradient.

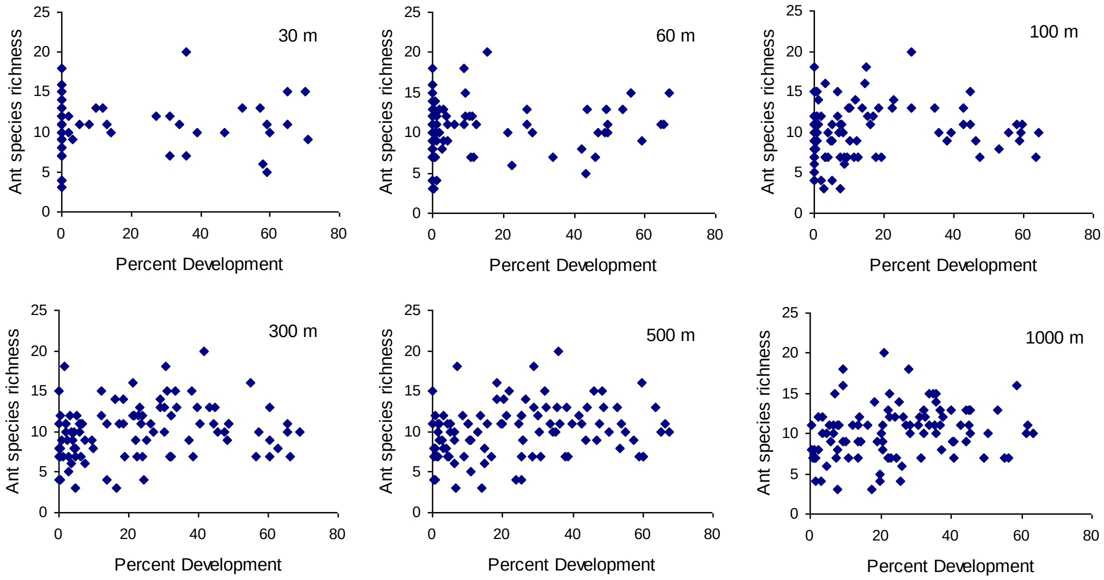


Figure 5.5. Ant species richness across the development gradient defined at six different scales: 30-m, 60-m, 100-m, 300-m, 500-m, and 1000-m scales.

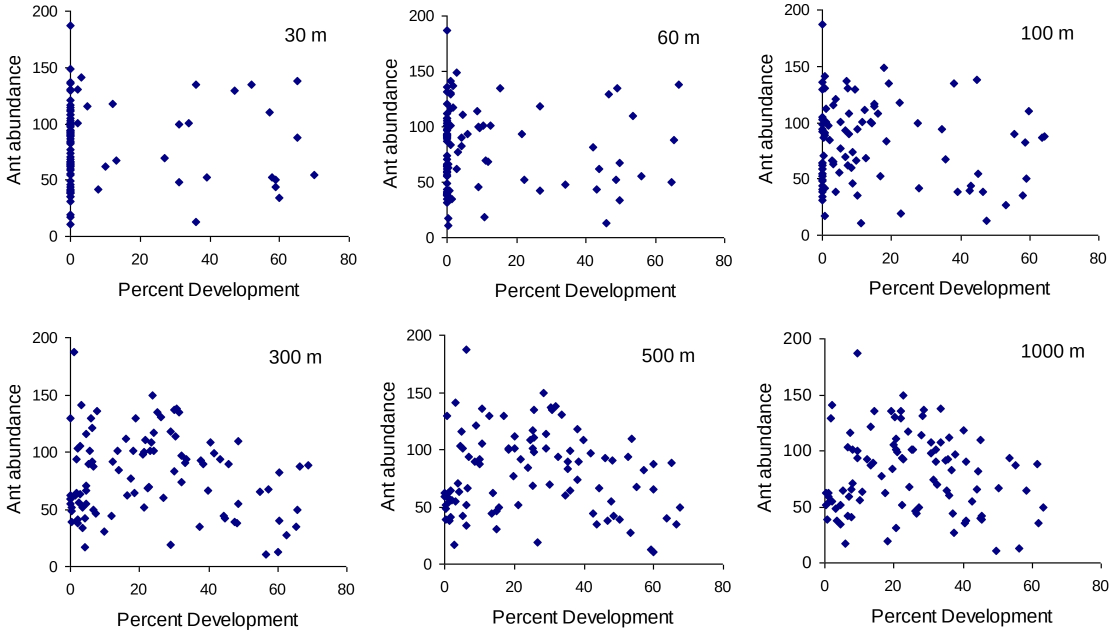


Figure 5.6. Total abundance of ants across the development gradient defined at six different scales: 30-m, 60-m, 100-m, 300-m, 500-m, and 1000-m scales.

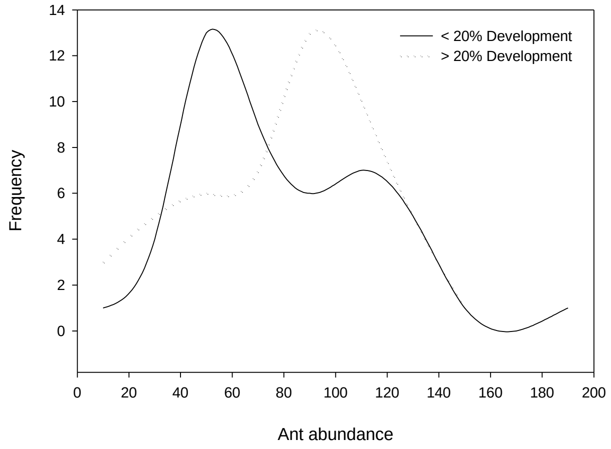


Figure 5.7. Frequency of occurrence of ant abundance values within two categories of percent development within 300 m.

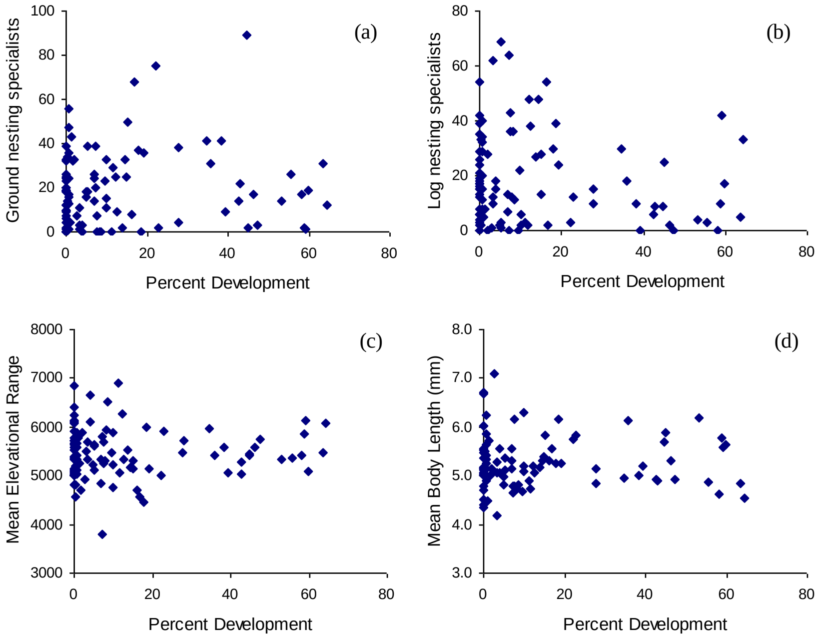


Figure 5.8. Ant abundance relative to percent development at the 100-m scale. (a) Abundance of ground nester specialists per site. (b) Abundance of log nester specialists per site. (c) Mean elevational range of species. d) Mean body length of species for each site.

Individual species responses to the multiple scales of urban development indicated that eight species were either negatively or positively affected by development (Appendix 5.1). Six of these species (*Camponotus vicinus (-), Formica accreta (-), Formica cf. sibylla (-), Formica ravida (+), Formica sibylla (+), and Temnothorax nitens (-)*) responded significantly to the 60-m scale of development; only two species (*Formica* cf. *sibylla (-), Formica ravida (+)*) had significant responses to the 100-m scale, two species (*Formica* cf. *sibylla (-), Formica ravida (+)*) to the 300-m scale, none to the 500-m scale, and two species (*Formica cf. sibylla (-), Formica neoclara (+))* to the 1000-m scale . We plotted adjusted R2 values against scale of development for six species (Fig. 5.9) and found that the 60-m scale on average explained 28% more of the variance in species abundances than 100-m scale (p = 0.139), 50% more than the 300-m scale (p = 0.023), 84% more than the 500-m scale (p = 0.018), and 74% more for the 1000-m scale of urban development (p = 0.035).

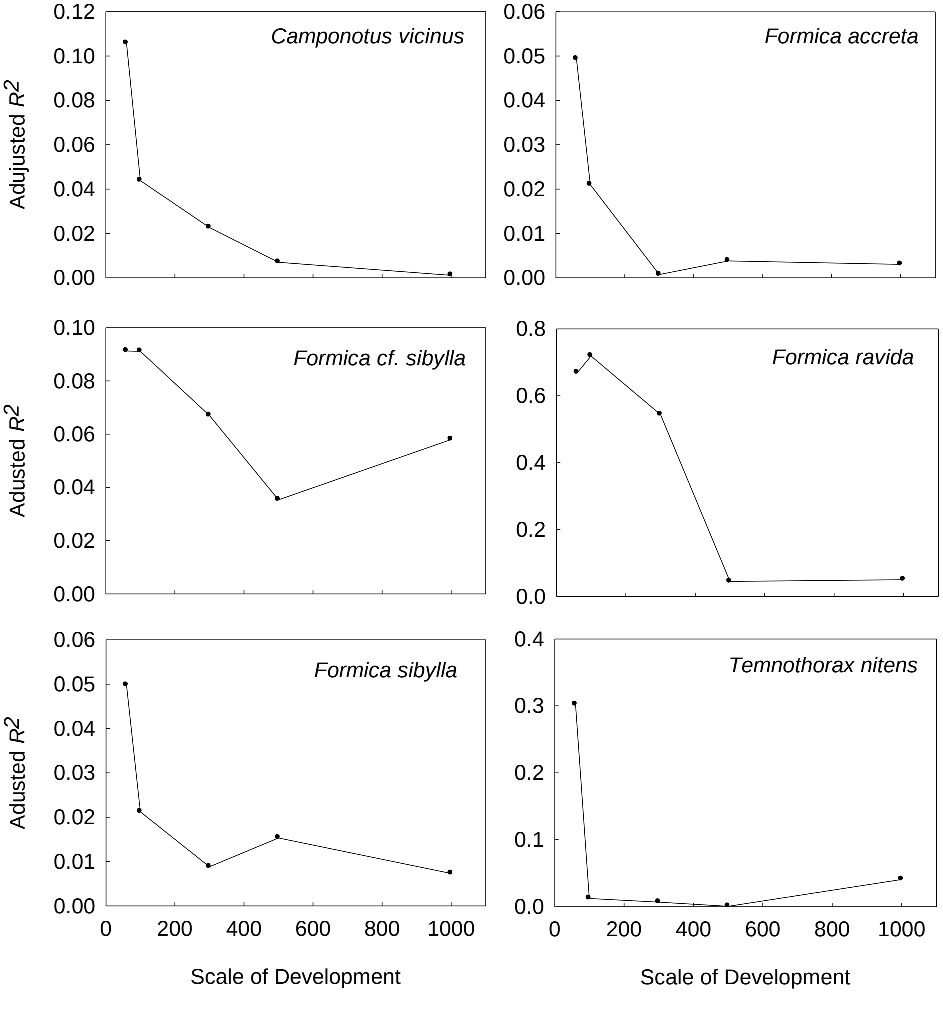


Figure 5.9. Species abundance responses to increasing scales of urban development. Adjusted R^2 values are from univariate regression analyses for each scale of development (60, 100, 300, 500, and 1000 m).

We also examined the distribution of rare and common species across the urban development gradient (Fig. 5.10). The frequency of least common (rare) species was greater in low development areas (< 20% development) ($X^2 = 8.85$, $df = 2$, $p < 0.025$), while only one species was found above 60% development. This indicates the strong tendency of rare species to occur only in low development areas. Examining distributions of the most common species indicates the ability of those species to use areas with a wide range of development.

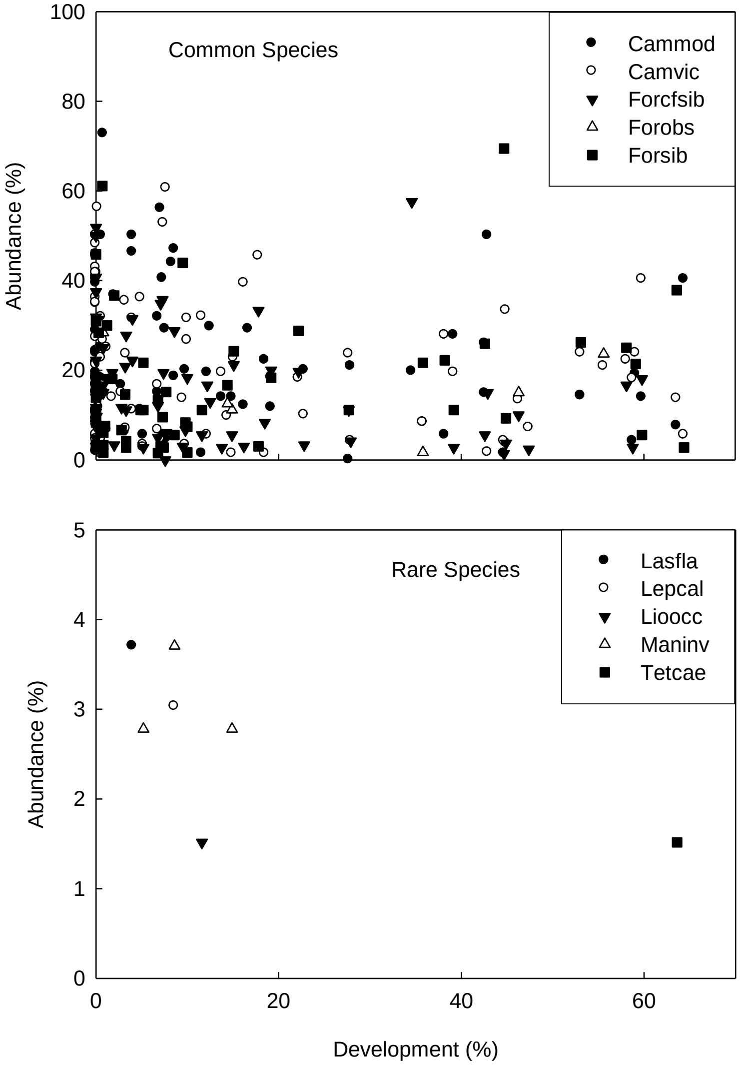


Figure 5.10. Abundance of rare and most common ant species as a function of percent development at the 100-m scale. Ant species names are given as the first three letters of the genus and first three of the species.

Small-scale Disturbance Patterns

Ant species richness declined significantly as the total area of compacted surface (from field-based vegetation measurements taken within 30 m of the center of the site) increased (r^2=0.20, df=26, P = 0.017; Fig. 5.11). Of the three vegetation parameters assessed (coarse woody debris, impervious surface, and tree density), only tree density elicited a response in ant species richness (P = 0.05).

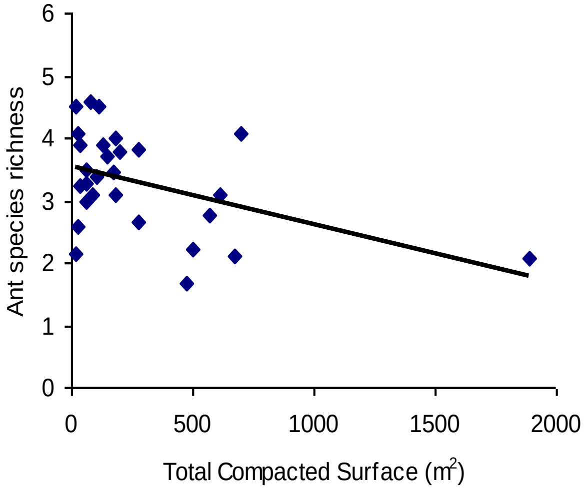


Figure 5.11. Ant species richness in response to total compacted ground surface at sites.

Ant richness peaked at moderate levels of site-specific (within trapping grids) disturbances (Fig. 5.12). Species richness differed significantly between ranked disturbance classes (0-2) (F = 4.96, df = 2, P = 0.009), with species richness in moderately disturbed sites 25% greater than in low disturbance sites and 10% greater than in high disturbance sites. Mean species per trap also differed significantly between disturbance classes (F = 4.16, df = 2, P = 0.019), but only with an 18% difference between moderate and low disturbance and no difference between moderate and high disturbance. Ant abundance was greatest in the moderate disturbance class, but did not vary significantly across disturbance classes (F = 0.92, df = 2, P = 0.39).

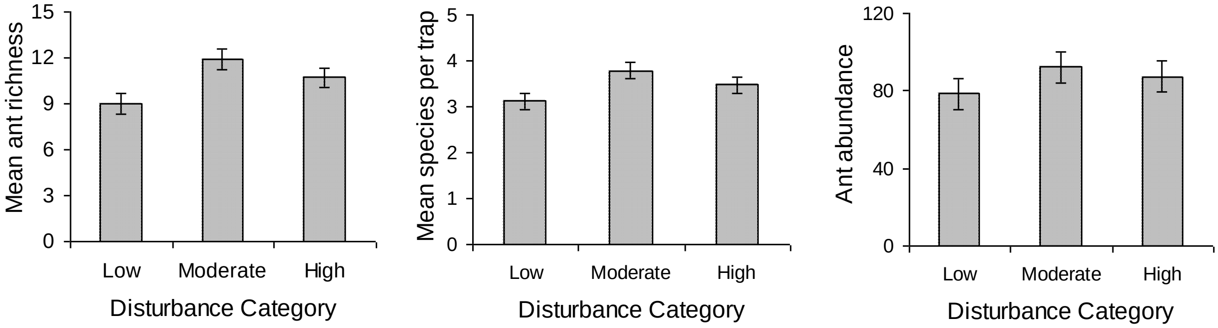


Figure 5.12. Patterns of site richness, richness per trap, and abundance along site-specific disturbance. n = 72 sites from 2003 sampling.

We also examined the effect of development types and distance on a small scale. A significant type by distance interaction was demonstrated (F = 3.48, df = 4, *P* = 0.028), but neither distance or type showed singular effects on species richness. At 0 m, species richness declined from highways, OHV, and residential developments, whereas the inverted pattern of species richness was observed at 100 m. A development type effect was observed for abundance (F = 6.437, df = 2, *P* = 0.008), while no distance effect was observed on abundance (*P* = 0.30). A significant type by distance effect on ant abundance was observed (F = 5.585, df = 4, *P* = 0.004). Abundance demonstrated the same inverted pattern between development types at 0 m (declining) and 100 m (increasing).

Discussion

The effects of urbanization on biodiversity have largely focused on areas with hardened boundaries between urban areas and wildlands. The relative muteness of boundaries between wildlands and urban forests in the Lake Tahoe basin has been thought to preserve biodiversity and forest health. However, few areas escape the impacts of human disturbance (Wilson 1989, Ojima et al 1991), and this research on ant communities demonstrates that biodiversity was impacted by development even within urban forests with muted boundaries. Koh and Sodhi (2004) found similar results where butterfly diversity was negatively affected even in forested parks adjoining larger wildlands. Thus, the effects of development and human disturbance not only impacts developed parcels, but have erosive effects on species and populations beyond developed lands.

Variations in urban development at multiple scales were associated with several measures of ant community structure, including species richness, abundance, composition of functional groups, and the abundance of individual species. Our results did not indicate declines in biodiversity and abundance across the development gradient. Rather, patterns of ant diversity and abundance demonstrate effects from site specific disturbance and larger scale urban development. The relationship between urban development and ant community structure varied depending on the scale of analysis.

Ant species richness was affected both by our measures of development and subsequent human uses within urban forests. Our multi-scale approach provides evidence for the intermediate disturbance hypothesis (Connell 1978). Peaks in species richness at moderate levels of urbanization have been observed previously in ants (Nuhn and Wright 1979) and other insect taxa (Pawlikowski and Pokomiecka 1990, Blair and Launer 1997, Blair 2001). The mechanism for greater ant richness at sites with intermediate levels of urban development may be caused from greater environmental heterogeneity that can support more species (Levin and Paine 1974, Laurance et al. 2002, McKinney 2002). Moderate levels of development may provide greater resources to sustain species since they provide components of natural habitats while also incorporating components of urban habitats that ants may use advantageously. Hence, ant species richness should be greater in areas where urban-avoiding ant species can be retained at sites with remnant habitat components, urban-adapting species can use both natural and urban resources, and urban-exploiting species can occupy urban habitat components.

Patterns of species dominance-diversity from high disturbance areas tend to have a steep declining curve, whereas areas of lower disturbance exhibit a progressive increase in community evenness with a slope closer to zero (Bazzaz 1975, Tokeshi 1993). Our data had only a minute reflection of such a pattern, whereby the dominance-diversity curve for low sites had only a slightly greater declining curve than did high disturbance sites. This pattern edges toward the niche preemption hypothesis (Motomura 1932, Whittaker 1965) where high disturbance sites contain dominant species that occupy a higher fraction of the total niche space within a community. This suggests that ant communities are impacted from development in such a manner that alters competition and resource use within communities.

We divided the ant species into numerous functional groups, but few of our functional groups of ants responded strongly to our index of urban development. Our classifications of functional groups were very limited because of the little published data on specific natural histories of the Tahoe ant fauna. Thus we were restricted to four functional group classifications. First, we predicted that highly developed areas would contain less structural habitat complexity that would cause a decline in log-nesting species. Log-nesting specialists demonstrated a response to development in the form of a declining power function. Although the abundance of log-nesting specialists was not correlated with the volume of coarse woody debris at our sites, the total compacted surface area negatively affected species richness of ants. Second, disturbed areas are predicted to contain species with greater body size (Southwood et al. 1979, Brown 1985, Steffan-Dewenter and Tscharntke 1997). However, we did not find evidence for this in our urban development study system. Third, we predicted that species with narrow elevation distributions would be affected more by development. However, our data indicate no pattern between elevational range of species and urban development. Fourth, ground-nesting species abundance was predicted to increase with development because forest in more urban settings to be more open and contain less coarse woody debris. We found no evidence for that hypothesis.

However, one important finding here was that rare native species were detected at sites with low development, while nonnative species were detected in high development areas. Disturbance ecology and successional theory both predict that native species are higher in diversity and dominance in less disturbed and old successional communities (e.g. Inouye et al. 1987). Our results also indicate that native rare species are more prone to extinction in high development urban forests and may have a reduced ability to colonize such areas especially given low populations (Pimm 1991, Denys and Schmidt 1998). Abundance of native ant species (excluding the nonnative *Tetramorium caespitum*) dropped with increasing development, and none of these rare native species were detected in urban forests where development was greater than 20%. This corroborates results from Koh and Sodhi (2004) who found more unique species in wildlands and parks adjoining wildlands compared to more isolated patches with greater urbanization influences. Nonnative species tend to increase with increasing urban development (Marzluff 2001) and our data support this given the observation of *Tetramorium caespitum* within a high development site. Thus, wildlands with low urban development provide important benefits for biodiversity, and high development sites, although harboring a diversity of species, provide zones for nonnative encroachment (see Blair 2001, Marzluff 2001).

Numerous ant species demonstrated strong responses to urban development at varying scales of resolution. Our 60-m scale of urban development explained the majority of variance for six species, and these species responded less strongly to greater resolutions of development (e.g., 100-m to 1000-m scales). Hence, these data indicate that not only are large-scale landscape models important in describing patterns of abundance and diversity of species, but that fine-scale resolutions can explain patterns of abundance and diversity for smaller organisms that comprise a large portion of biodiversity but are often overlooked in larger-scale research.

Several implications for conservation and land-use planning of urban forests in the Tahoe Basin may be drawn from this study. Ant species richness was highest in forests of moderate levels of urban development and low development sites contained many unique species, implying that areas containing low to moderately urbanized landscapes are the most valuable for conserving species diversity, and therefore should be given highest conservation priority. This corroborates findings from other taxonomic groups from this LTUB research. Although high development sites comprise native fauna, our ant data indicate that these sites harbor nonnative species and they may provide the basis for nonnative encroachment. The Tahoe Basin has been relatively buffered from the encroachment of nonnative species, especially given its montane-basin setting between two geographic zones with very pervasive problems regarding nonnative invasive species. The coupling of global climate change and human-induced species changes should be cause for concern in the basin, and we suggest conservation measures should hinder these potentially large future problems. Further, institutional conservation responses should maximize native biodiversity protection, while minimizing opportunities for nonnative species.

Chapter 6: Plants

Introduction

Fragmentation of the landscape produces remnant vegetation patches surrounded by a matrix of different vegetation type or land use. The primary effects of this are changes in microclimate within the fragment and isolation of each patch from other patches (Saunders et al. 1991). A myriad of dynamics can occur when forests are fragmented, depending on the ecosystem and nature of the disturbance. For example, fragmented forests may have reduced richness of native species, particularly specialist species that rely on one or more forest features that are sensitive to disturbance, and they may experience higher disturbance rates, shifting the competitive regimes to favor exotic or matrix species (Debinski and Holt 1998). Forest fragments with a high edge-to-area ratio are more vulnerable to invasion by exotic or matrix species and are subject to more extreme abiotic factors such as wind and temperature (Saunders et al. 1991).

In cases where there are less dramatic differences between matrix and fragments such as in the Lake Tahoe basin, the ecosystem effects are expected to be less noticeable. Vegetation in sites with high surrounding development are predicted to have fewer native species, more exotic species, more shade-intolerant or early successional species, lower density of understory vegetation, reduced recruitment of disturbance-sensitive tree species, and higher incidence of conifer pathogens compared to sites in similar vegetation types but with little or no surrounding development. We also predict that many environmental factors other than development (e.g., logging history, fire suppression, local variation in precipitation and weather, and edaphic factors) contribute to the current condition of sites. Thus, site location, type, and history are all likely to affect the relative and absolute impact of current levels of development and human disturbance.

Methods

Data Collection

Vegetation was characterized using a combination of U.S. Forest Service procedures (Casey et al. 1995) and standard botanical survey methods. The sampling design had four primary components (Fig. 6.1).

- Three line-intercept transects (30 m) to estimate percent ground cover, volume of coarse woody debris, litter depth, soil compaction, and to characterize the physiognomy of vegetation layers.
- Four circular subplots (7.3 m radius) used to estimate percent cover of trees, shrubs, and exotic species.
- Twelve quadrats ($1m^2$) used to estimate percent cover of herbaceous plants and shrubs.
- Three concentric circular plots (7.3m radius, 17.6m radius, and 56.4m radius) used to describe forest stand structure.

The sampling methods were conducted at each site's center point, which was permanently marked with rebar. This point served as the starting point for all transects and the center of the three concentric circles.

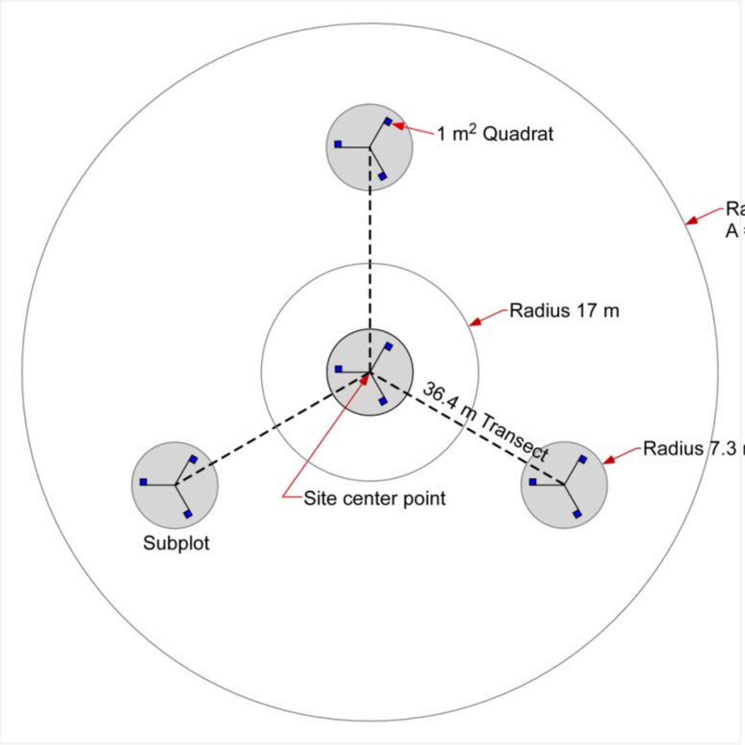


Figure 6.1. Layout of subplots, quadrats, and transects employed at the center point of Lake Tahoe Urban Biodiversity project in 2003.

At the site center point, the following general information was collected: percent slope angle measured with a clinometer; slope aspect; human disturbance by type within 30 m of center point; distance to all roads or trails within 100 m of the center; distance to water within 100 m; and distance to riparian vegetation within 100 m.

Along each of the three 30 m transects (Fig. 6.1), the following information was collected:

- Percent Ground Cover. Ground cover estimates were made at every third meter, for a total of 10 one meter long segments along each transect. For each segment, the length of all plant species and non-vegetative ground cover (bare soil, litter, rock, coarse woody debris) that intersected the transect tape was measured.
- Physiognomy. Vertical structure of the plant community was described using the point intercept method along the three transects. Measurements were made every third meter, for a total of 10 sample points. All plant species intersecting the transect tape at any height above the point on the tape were recorded.
- Litter Depth and soil compaction. Litter depth and soil compaction measurements were taken at the same 10 point intercept locations used to sample vertical structure.

- Coarse Woody Debris. Volume and decay class (Casey et al. 1995) of coarse woody debris (logs > 10 cm diameter) were characterized along the three transects. Volume was calculated from the two end diameters and length of the log.
- Anthropogenic Features. The length and type (trail, dirt road, paved road, highway, ski lift, parking lot, house, or campsite) of anthropogenic feature were recorded for each transect.

Four, 7.3 meter subplots were established at each site (Fig. 6.1). Cover of each tree, shrub, and non-native plant species in the subplot was estimated to the nearest 1%. Each subplot was searched for 15 minutes in order to list all species present. Within each subplot, percent cover of all plant species was estimated in three 1 m^2 quadrats.

Three nested circular plots were used to describe forest tree structure at each site: 1 ha (56.4 m radius circle), 0.1 ha (17.6 m radius circle), and 0.017 ha (7.3 m radius circle) plots (Fig. 6.1). Within each circular plot, the following information was recorded for trees and snags: species, height to nearest meter using a clinometer, diameter at breast height using a DBH tape, decadence code for live trees (Table 6.1), and decay class (Casey et al. 1995) for snags. Measurements for the three circular plots are restricted to certain DBH classes of trees and snags: in the 7.3 m radius circle we measured all trees and snags >12.5 cm diameter; in the 17.6 m radius circle, we measured trees > 28 cm and snags > 12.5 cm diameter; and in the 56.4 m radius circle, we measured trees > 61 cm and snags > 30.5 cm diameter. In addition, sapling densities were recorded, by species, in the 7.3 m radius circle. The 17.6 m radius plot was used to measure canopy cover, with a moosehorn device, at four locations; the number of cut stumps by decay class; the number of pieces of trash; and the area occupied (in m^2) by anthropogenic features such as trails, dirt roads, paved roads, highways, and parking lots.

Table 6.1. Decadence codes for live trees measures in the Lake Tahoe Urban Biodiversity Project sites.

Decadence code	Decadence feature
1	Conks, bracket fungi
2	Cavities greater than 6 inches in diameter
3	Broken top
4	Large (> 12 inches in diameter) broken limb
5	Loose bark (sloughing)
6	Mistletoe
7	Dead top
8	Split top
9	Thin canopy (relative to neighboring trees)
10	Light foliar color
11	Leaf necroses
12	Frass
13	Sap exudation

Data Analysis

Forest Structure and Health

Simple linear regressions, using JMP version 5 (SAS Institute Inc. 2003), tested the effects of urbanization on forest structure. Urban development, the independent variable, was regressed on following dependent variables: average percent canopy cover; estimated density of trees per hectare; estimated basal area of trees per hectare; height class diversity (defined here as the number of height classes occupied by vegetation, where height classes were 0-1 m, 2-3 m, etc. above ground.); estimated snag density per hectare; estimated snag volume per hectare; average decay class for snags; volume of coarse woody debris; average decay class for coarse woody debris; and number of cut stumps. Volume was used for snags, instead of basal area, because it accounts for the fact that snags can be broken off at various heights. Simple linear regression determined whether development was correlated to percent of trees showing disease symptoms or to soil compaction.

In addition to analyzing site centers, we also measured vegetation characteristics at the satellite point count stations (4 per site) located 250 meters away from the site center. These satellite sites represent the landscape at large below 7000 ft in elevation. We compared the conditions of native forests to sites not constrained to occur within native forest to determine the degree to which native forests retained natural conditions.

Species Richness and Abundance

To understand the effects of urbanization on community composition, simple linear regressions were done between development (independent variable) and species richness, diversity, and percent cover for: all species, all native species, all exotic species, native and exotic annual herbs, perennial herbs, annual grasses, perennial grasses, shrubs, and trees (dependent variables). To test whether rare (occurring in fewer than 5% of the sites) native species were affected by development, both number and proportion of rare native species per site were regressed on development. Only taxa identified to species were considered for this analysis.

Species Turnover

To look for trends in species turn-over along the development gradient, frequency of occurrence was examined for each species. First, sites were divided into 5 categories, with equal intervals of development, and the proportion of sites having each species was calculated for each category. Second, data were visually inspected for species with strong trends in frequency along the development gradient. Only species found in ≥ 15 sites were selected for further examination because reliable patterns could not be detected for rarer species. Third, of the twenty-one species showing clear trends, logistical regression was used to explore the relationship between development and species presence/absence. Old-growth sites were excluded because they represent only low development, west-basin sites. Because 21 analyses were done simultaneously, a Bonferroni adjustment was applied, thus reducing the critical p-value to 0.002 (0.05/21). Logistic regressions were also used to test whether number of people per hour or number of unrestrained dogs per hour affected species presence/absence.

Species Packing

Species-abundance curves were used to compare species-packing between low (0-34%, 83 sites) and high (35-70%, 35 sites) development sites. Relative percent cover data were used to create species-abundance curves for herbs and grasses, shrubs, and trees. Species were grouped by life-form to avoid comparing species with large size or percent cover differences. For each species, percent cover data were averaged across all sites, relativized, and $\log_{10}$ transformed. Relative percent cover estimates were ranked from 1-n (most common to least common). Species with the same relative percent cover were given the same rank. Rank-abundance curves were created to assess species-packing patterns.

Community Ordination and Variance Partitioning

To test whether urbanization had a significant influence on plant community composition, variance partitioning was used to separate the effects of human-caused (H) and naturally occurring (E) environmental variables. Canonical Correspondence Analysis (CCA) was chosen for its ability to utilize covariables, a necessary part of variance partitioning, and test for statistical significance. CCA is a direct gradient analysis that relates species composition to selected environmental variables, while ignoring community structure unrelated to these variables (McCune and Grace 2002). CCA was performed with default settings by Canoco 4.5 and CanoDraw 4.0 for windows (ter Braak and Smilauer 2002).

Two matrices were used for analysis: the species matrix and the environmental variable matrix. The species matrix of average percent cover values had 116 sites and 69 common species. Deletion of rare species, occurring in 5% or fewer sites, is recommended for reduction of noise without losing the bulk of the information in a dataset (McCune and Grace 2002). The environmental variable matrix (116 sites and 13 variables) contained all (E) and (H) variables. (H) included percent development, GIS-modeled percent impervious surfaces, number of unrestrained dogs per hour, number of people per hour, and number of vehicles per hour. (E) included easting (UTM zone 10, NAD 27); GIS-modeled elevation; GIS-modeled aspect (transformed according to Beers et al. 1966, ranging from 0 (southwest) to 2 (northeast)); date of final snow-melt, in Julian days, developed specifically for the Tahoe Basin by Royce (earlier versions of the model in Royce 1997 and Barbour et al. 1998); GIS-modeled soil wetness; GIS-modeled heat load index; and GIS-modeled average annual precipitation. All GIS-modeled variables were calculated according to Parks et al. (in press).

Three separate CCA ordinations were preformed in the variance partitioning:
(1) CCA with all environmental variables (both E and H) and no covariates. This provided the total inertia (similar to variance) of the dataset.
(2) CCA of E with H as covariates. This removed the effects of the human-caused variables from the effects of the environmental variables.
(3) CCA of H with E as covariates. This removed the effects of the environmental variables from the human-caused variables.

From these analyses, I calculated the percent variance explained: uniquely by (E), uniquely by (H), jointly by (E) and (H), and by neither subset (methods according to Palmer 2005). This, and similar methods of variance partitioning, are well-documented in the ecological literature (Borcard et al. 1992, Jean and Bouchard 1993, Okland and Eilertsen 1994, Birks 1996, Ohmann and Spies 1998).

Results

Sampling Effort

In the 2003 and 2004 field seasons, we sampled 107 sites along the development gradient plus an additional 11 old-growth sites, originally identified by Barbour et al. (2002). The purpose in including the old growth sites was to extend the low development end of the gradient and to compare community composition between urban, seral forests and remote, unlogged forests. No additional data collection is planned based on current funding levels.

A total of 387 taxa were recorded in 118 sites, including 25 unknowns. The five most common species were *Pinus jefferyi* (n = 114 sites), *Abies concolor* (n = 105), *Arctostaphylos patula* (n = 82), *Gayophytum diffusum* (n = 81), and *Carex rossii* (n = 75). A large proportion (72%) of recorded species were rare, defined here as occurring in 5% (6) or fewer sites, while only 3% of species occurred in 50% or more sites.

Analysis Scale for Development

To determine the scale at which vegetation conditions are associated with development, relationships were explored using simple linear regression between various vegetation measures and percent development at 4 different scales: 100, 300, 500, and 1000 m radii. With a few minor exceptions, conclusions were the same for all four scales (Table 6.2). For those correlations having significant results, coefficients of determination varied little among the scales.

We chose to use the 300 m development index for data analyses for the following reasons:

1) The choice of scale does not appear to affect the conclusions reached about relationships between vegetation and development (Table 6.2);
2) It is intuitively reasonable to use a small scale for plants because of their sedentary lifestyle; environmental influences within close proximity should be more important than those far away; and
3) The sampling frame was designed using a 300 m buffer, so it is reasonable to use this scale for data analysis.

Therefore, all the following analyses are based on the 300 m development index.

Table 6.2. Correlations between various vegetation measures and percent development at four scales: 100, 300, 500, and 1000 m radii.

	DEV_100M	DEV_300M	DEV_500M	DEV_1000M
Total spp richness	NS	Positive (r^2 = 0.043)	Positive (r^2 = 0.045)	Positive (r^2 = 0.038)
Native spp richness	NS	NS	NS	NS
Exotic spp richness	Positive (exponential)	Positive (exponential)	Positive (exponential)	Positive (exponential)
Annual herb richness	NS	Positive (r^2 = 0.04)	Positive (r^2 = 0.04)	NS
Perennial herb richness	NS	NS	NS	NS
Shrub spp richness	NS	NS	NS	NS
Tree spp richness	NS	NS	NS	NS
Total tree density	NS	NS	NS	NS
Total tree BA	NS	NS	NS	NS
Total snag density	Negative (r^2 = 0.17)	Negative (r^2 = 0.22)	Negative (r^2 = 0.2)	Negative (r^2 = 0.21)
Total snag volume	Negative (r^2=0.25)	Negative (r^2 = 0.33)	Negative (r^2 = 0.3)	Negative (r^2 = 0.31)
Ave. snag decay	Negative (r^2 = 0.11)	Negative (r^2 = 0.08)	Negative (r^2 = 0.06)	NS
Volume of CWD	Negative (r^2 = 0.17)	Negative (r^2 = 0.22)	Negative (r^2 = 0.19)	Negative (r^2 = 0.17)
CWD decay	NS	NS	NS	NS
Soil compaction	NS	NS	NS	NS
Litter depth	NS	NS	NS	NS

Community Structure and Composition

There was no significant correlation between native species richness (square-root transformed) (P = 0.15), native shrub species richness (P = 0.5), native tree species richness (P = 0.2), native annual herb richness (P = 0.14), or native perennial herb richness (P = 0.34) and development. However, native perennial grass richness was positively correlated with development (r^2 = 0.14, $P < 0.001$). as was cover (r^2 = 0.13, $P < 0.001$). This pattern held for east sites (r^2 = 0.16 for richness, r^2 = 0.13 for average percent cover), but was only significant for average percent cover in west sites (r^2 = 0.13). There were no native annual grasses found in the study, so this analysis was not done.

There was no correlation between native (P = 0.86) or exotic (P = 0.16) species richness and the number of people per hour present in the site. Nor was there any correlation between native (P = 0.98) and exotic (P = 0.78) species richness and number of unrestrained dogs per hour.

Total exotic species richness (Fig. 6.2), exotic annual herb richness, exotic annual grass richness, exotic perennial herb richness, and exotic perennial grass richness were all positively correlated with development. All of these relationships are non-linear and, therefore, linear regression analysis was not applied. Exotic plant species richness exhibited a geometric increase in response to development, with rapid increases observed above 30% development. Sample sizes for exotic shrubs (n = 4) and trees (n = 6) species were not large enough for regression analysis. All exotic shrub and tree species found were cultivated or escaped ornamentals growing in or near yards.

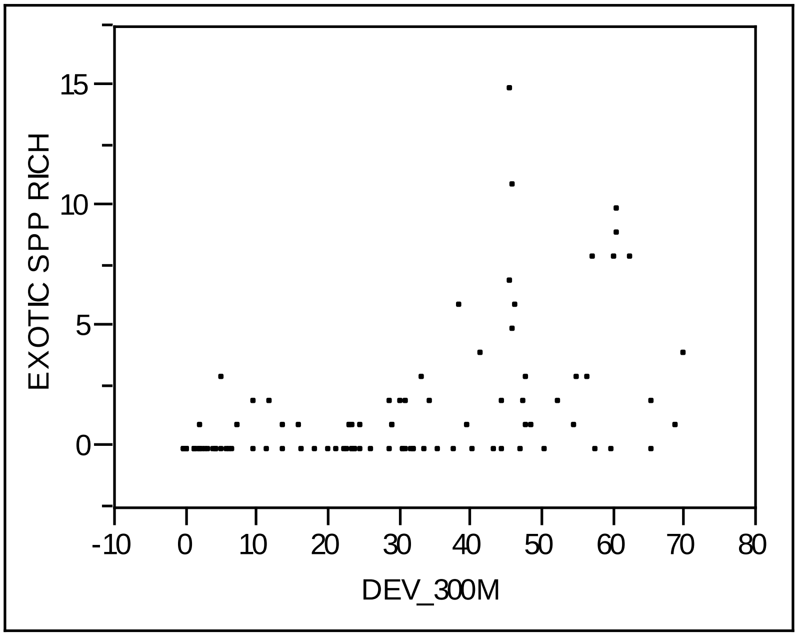


Figure 6.2. Scatterplot of exotic species richness by development.

A total of 41 exotic species were found, not including ornamental garden plants. The five most common exotic species were: *Bromus tectorum* (18 sites, 8-80% development), *Dactylis glomerata* (17 sites, 5-72% development), *Taraxicum officinale* (15 sites, 0-73% development), *Elytrigia pontica* (11 sites, 5-63% development), and *Polygonum arenastrum* (8 sites, 33-63% development). Forty-three of the 118 sites surveyed (36%) had exotic species. Sites having development values below 42% had low numbers of exotic species (0 to 3), while sites with development values over 42% had greater variation (0 to 15).

Average percent cover of native shrubs (*P* = 0.56), perennial herbs (*P* = 0.19), and annual herbs (*P* = 0.26) was not correlated with development. However, average percent cover of native trees was negatively correlated ($r^2 = 0.07$, $P < 0.001$) and average percent cover of native perennial grasses was positively correlated ($r^2 = 0.13$, $P < 0.0001$) with development. All percent cover values were square-root transformed to achieve normality.

Species Turnover and Packing

Of the 21 species tested for a relationship between occurrence and development, 7 had significant *P* values (Figure 6.3). Results showed that the probability of occurrence increased with development for: native perennial grasses *Festuca idahoensis* ($r^2 = 0.17$), *Poa secunda* ($r^2 =$

0.14), and *Elymus elymoides* ($r^2 = 0.12$); exotic perennial herb *Taraxacum officinale* ($r^2 = 0.17$); and exotic perennial grass *Dactylis glomerata* ($r^2 = 0.15$). Probability of occurrence decreased for native shrubs *Arctostaphylos nevadensis* ($r^2 = 0.13$) and *Chrysolepis sempervirens*, ($r^2 = 0.10$). None of the 21 species' occurrences were significantly correlated with number of people or unrestrained dogs per hour.

For herbs and grasses, the two trend-lines were almost identical, suggesting that species abundance patterns were not different for the two development categories (Figure 6.4). For both shrubs and trees, slopes for the low development groups were slightly steeper than those of the high development groups, but not different enough to have ecological consequences (Figures 6.4).

Forest Structure

Total estimated density of trees, >12.5cm dbh, per hectare, was not correlated with development ($P = 0.53$). Broken into size classes, estimated density of small trees per hectare, 12.5-27 cm dbh, ($P = 0.17$), estimated density of medium trees per hectare, 28-60 cm dbh, ($P = 0.63$), and density of large trees per hectare, >61 cm dbh, ($P = 0.90$) were not significantly correlated with development; however small tree density did decline with development. Tree density was square-root transformed for all analyses. These results suggest that development does not affect total tree density, but it appears to have an increasing effect on the density of smaller diameter trees.

Total estimated basal area of trees, >12.5 cm dbh, per hectare, was not correlated with development ($P = 0.54$). Broken into size classes, basal area of large trees, ≥ 61 cm dbh, per hectare ($P = 0.78$), estimated basal area of medium trees, 28-60 cm dbh, per hectare ($P = 0.45$), and estimated basal area of small trees, 12.5-27 cm dbh, per hectare ($P = 0.34$) were not correlated with development. Basal area was square-root transformed for large, medium, and small trees.

Average number of height classes encountered (square root transformed) in a site was not significantly correlated with development ($r^2 = 0.026$, $P = 0.08$); however it did decline with development. Height class diversity was defined as the number of height intervals (an example height interval is 0-1 m above the ground) occupied by vegetation.

Total estimated density of snags, >12.5 cm dbh, per hectare, was significantly negatively correlated with development ($r^2 = 0.22$, $P < 0.0001$). In addition, variance of snag density decreased with increasing development. Development was negatively correlated with density of large snags, >30.5 cm dbh ($r^2 = 0.36$, $P < 0.001$), and small snags, < 30.5 cm dbh ($r^2 = 0.067$, $P = 0.007$). Densities for total and large snags were square root transformed to achieve normality.

Total estimated volume of snags per hectare was negatively correlated with development (Fig. 6.5). Volume was calculated by multiplying basal area by height. Volume was used for snags, instead of basal area, because it accounts for the fact that snags can be broken off at various heights. Basal area tends to over-estimate the amount of standing dead wood. Both total estimated volume and variance decreased with development.

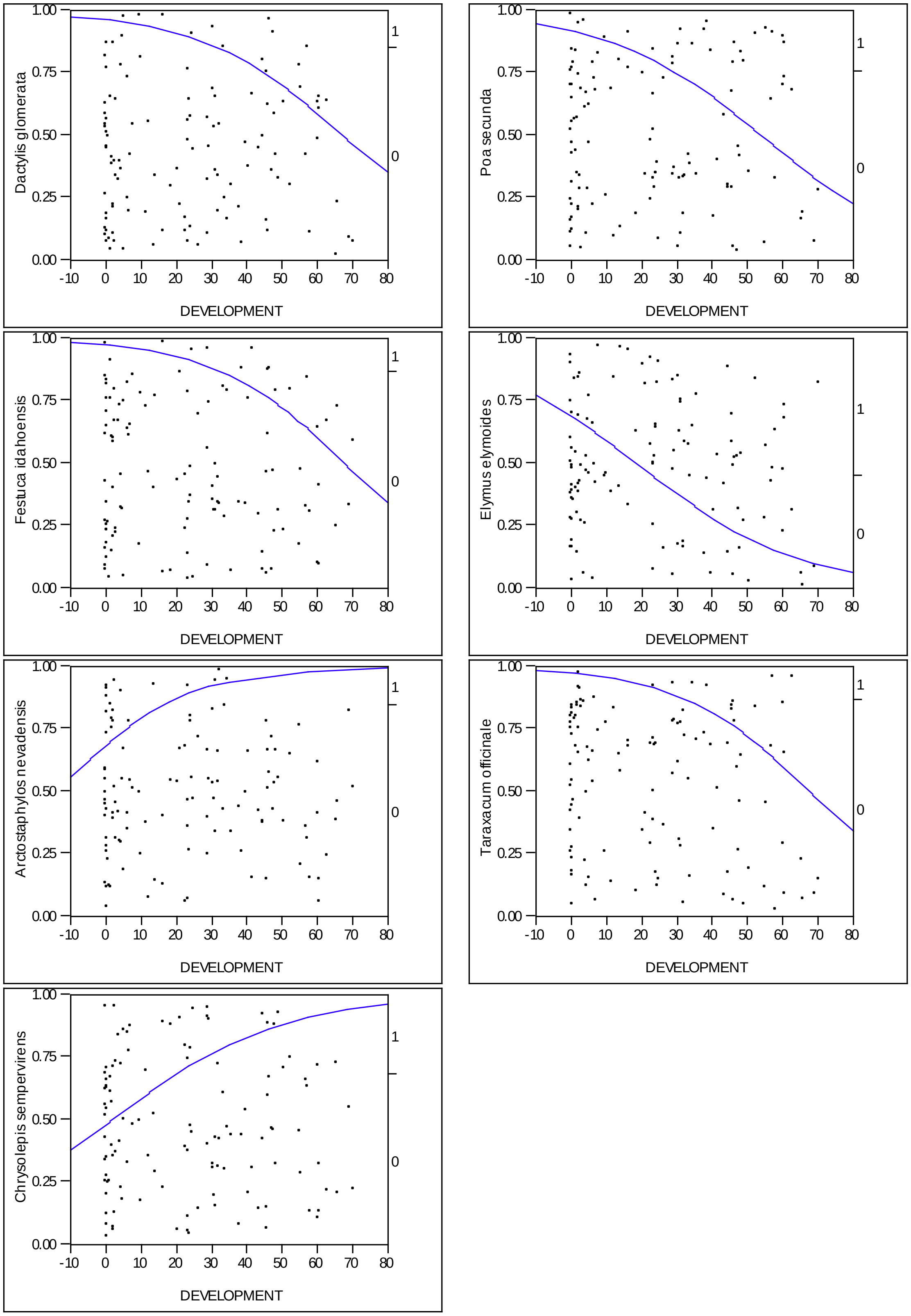


Figure 6.3. Logistic regressions for absence (0) or presence (1) of 5 species.

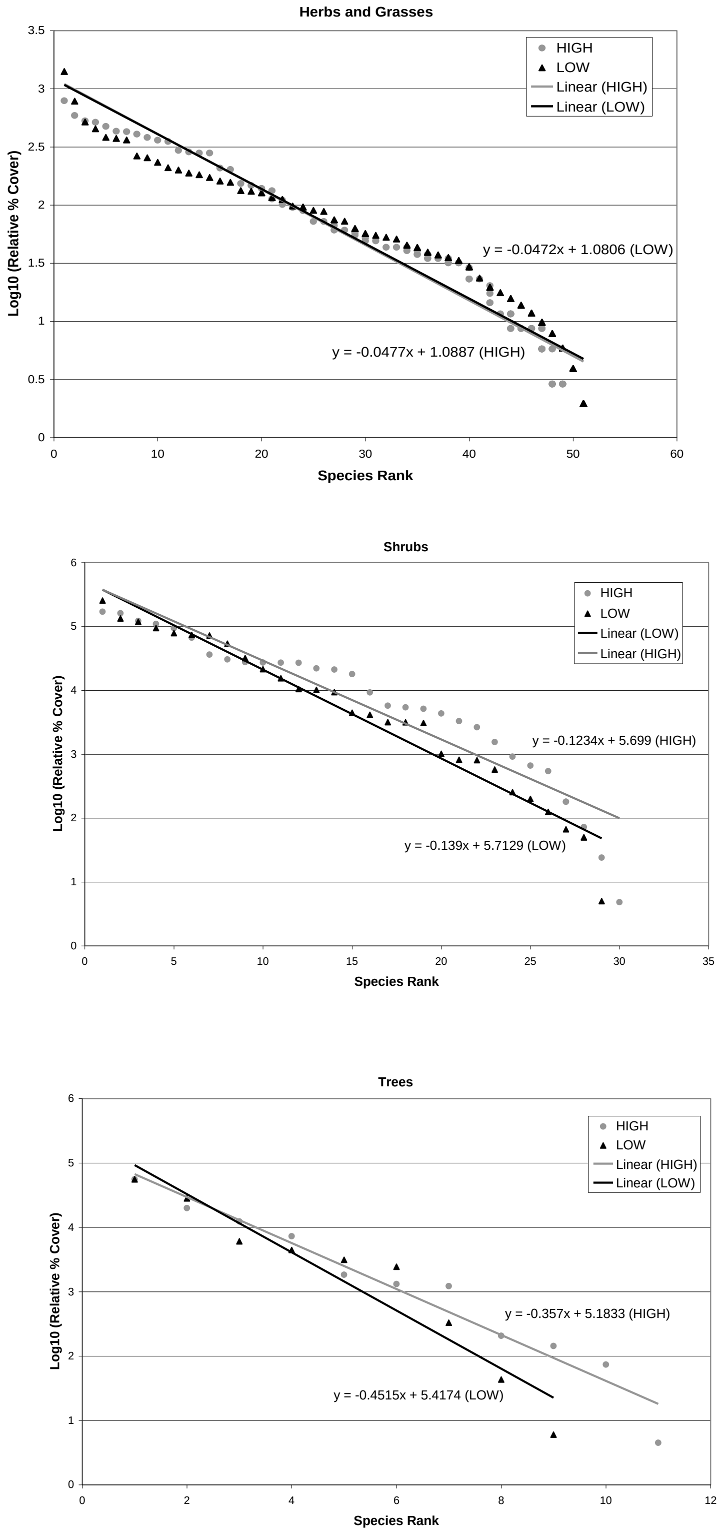


Figure 6.4. Species rank vs. log (10) relative percent cover for herbs and grasses, shrubs, and trees in high (35-70%) and low (0-34%) development categories. Note: linear regression trend-lines in herbs and grasses are overlapping.

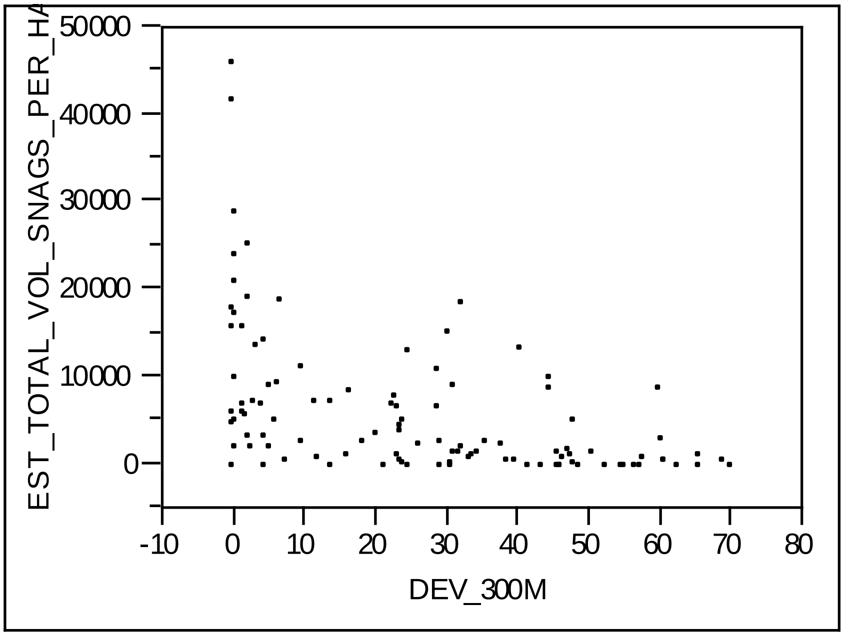


Figure 6.5. Scatterplot of estimated total volume of snags (m^3) per hectare by development.

Number of cut stumps (log transformed) was slightly positively correlated with development ($P < 0.0001$, $r^2 = 0.17$) (Fig. 6.6). The frequency of occurrence of cut stumps at a site increased with development; above 50% developed sites generally had some cut stumps, evidencing the occurrence of recent management.

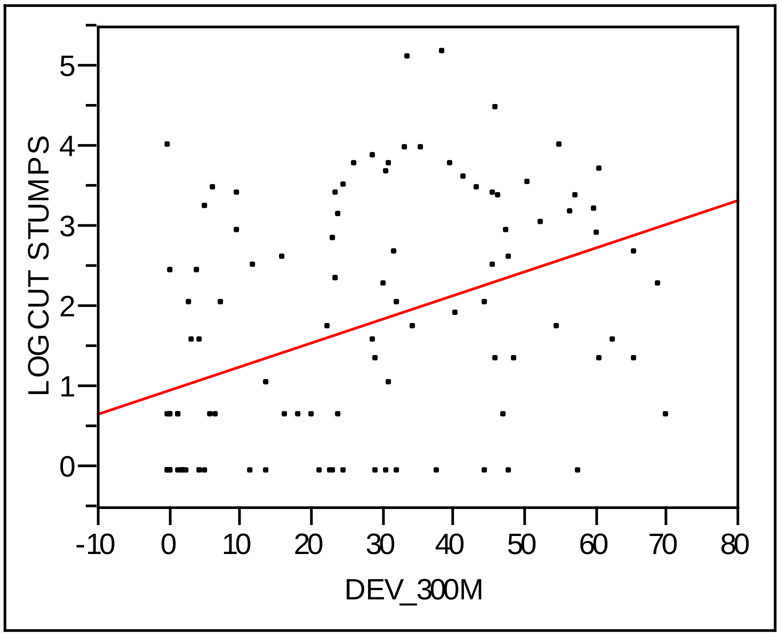


Figure 6.6. Simple linear regression of number of cut stumps (log transformed) by development.

Average snag decay class (1-5) was slightly negatively correlated with development (P = 0.005, r^2 = 0.08) (Fig. 6.7). Less developed sites generally had older, more decayed snags than more developed sites, with the trend suggesting a steady decline in the prevalence of more decayed snags with greater surrounding development.

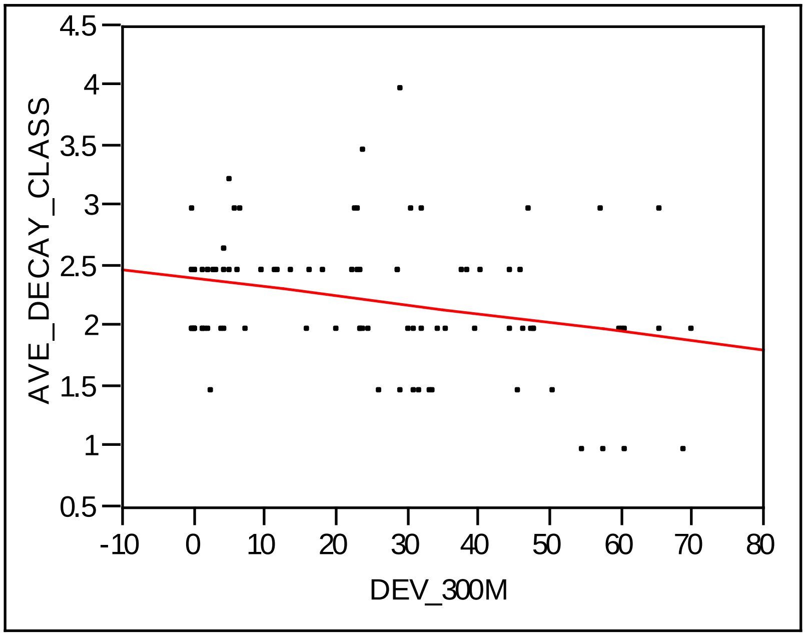


Figure 6.7. Simple linear regression of average snag decay class (1-5, one being least decayed and 5 being most decayed) by development.

Volume of coarse woody debris (log transformed) was negatively correlated with development (r^2 = 0.2, $P < 0.001$) (Fig. 6.8). Volume of coarse woody debris ranged from 0 m^3 to 56 m^3, encountered along 90 meters of transect in each site. Variance was high at the lower end of the development gradient, but decreased sharply in the upper end of the gradient. This indicates that the volume of coarse woody debris was quite variable in low to moderate development sites, but was consistently low in high development sites, particularly at sites surrounded by > 40% development.

Simple linear regression was used to determine if there was a relationship between development and average decay class of coarse woody debris (on a scale of 1-5, one being the least decayed and 5 being the most decayed). Analysis showed no correlation (P = 0.21).

Average soil compaction (P = 0.15) and average litter depth (P = 0.59) were not correlated with development. Soil compaction was not correlated with number of people per hour (P = 0.72), number of dogs per hour (P = 0.70), or number of unrestrained dogs per hour (P = 0.81). Our measure of soil compaction was not highly sensitive, so this negative result is not conclusive.

The comparison of undeveloped forests to the landscape-at-large along the development gradient revealed that remnant undeveloped forests retained many of their natural characteristics at higher levels of development compared to the landscape-at-large (Fig. 6.9). Although canopy cover did not vary significantly with development in native forests, it was significantly lower throughout the landscape (adj. R^2 = 0.119, $P < 0.001$) at higher development. Similarly, tree densities did not vary significantly with development in native forests; however, in the landscape-at-large, the densities of small (>12.5-27 cm dbh) and medium (28-60 cm dbh) diameter trees density were significantly lower in areas with higher development (adj. R^2 = 0.140, *P* < 0.001, and adj. R^2 = 0.204, *P* < 0.001, respectively). Interestingly, large tree (>61 cm dbh) density in the landscape-at-large did not change significantly with development (P = 0.296), but native forests had a lower range of tree densities than the larger landscape (Fig. 6.9).

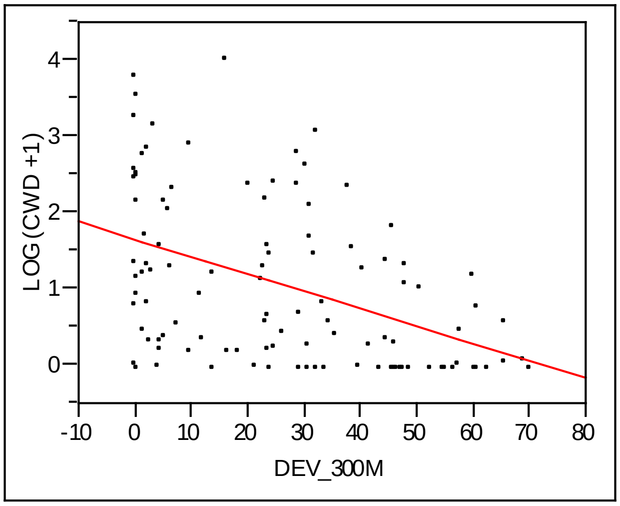


Figure 6.8. Simple linear regression of volume of coarse woody debris, measured in m^2/ha, by development.

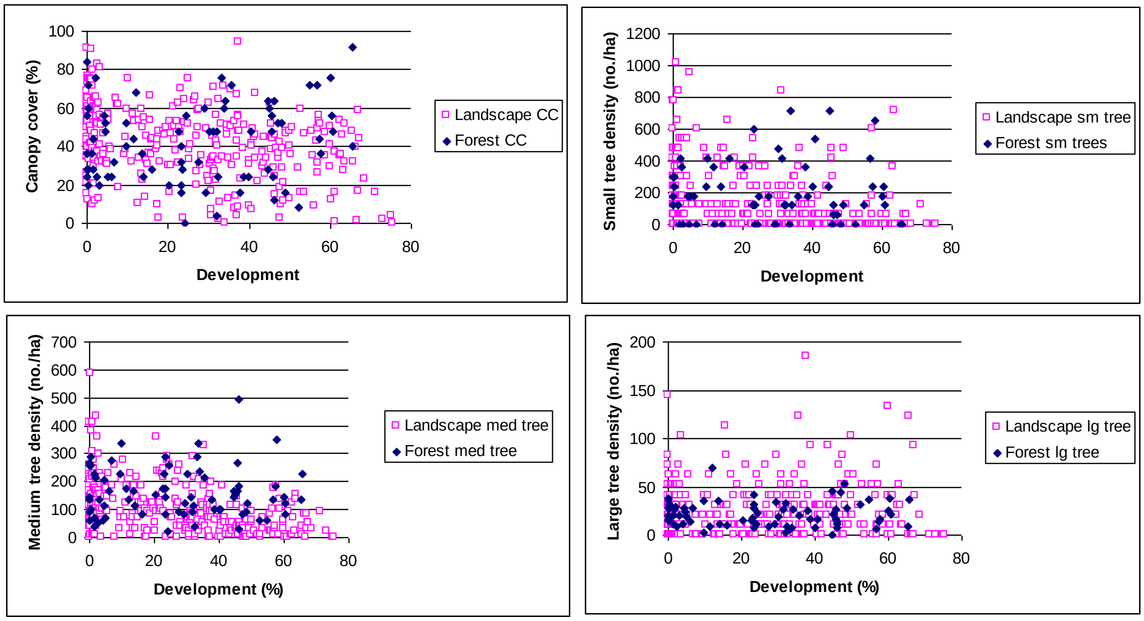


Figure 6.9. Scatter plots showing the relationships between vegetation characteristics and development for two types of sites: native forests and throughout the landscape. Data were collected at 375 sites below 2100 m in elevation in the Lake Tahoe basin in 2003-2005.

Native forest and the landscape-at-large both showed declining snag and log densities as development increased (Fig 6.10). At lower levels of development, small and large snag densities had a higher range of values in the larger landscape compared to native forests. This is most likely an artifact of the larger sample size for landscape sites compared to native forest sites (300 vs. 75, respectively). Shrub cover declined significantly in landscape sites with increasing development, unlike native forest sites which showed no change in shrub cover. Sites in the larger landscape had a wider range of shrub cover values, most likely reflecting the occurrence of sites in shrub-dominated vegetation. Herbaceous plant cover did not decline significantly in the larger landscape or native forests, and it appeared to have similar values between the two groups of sites.

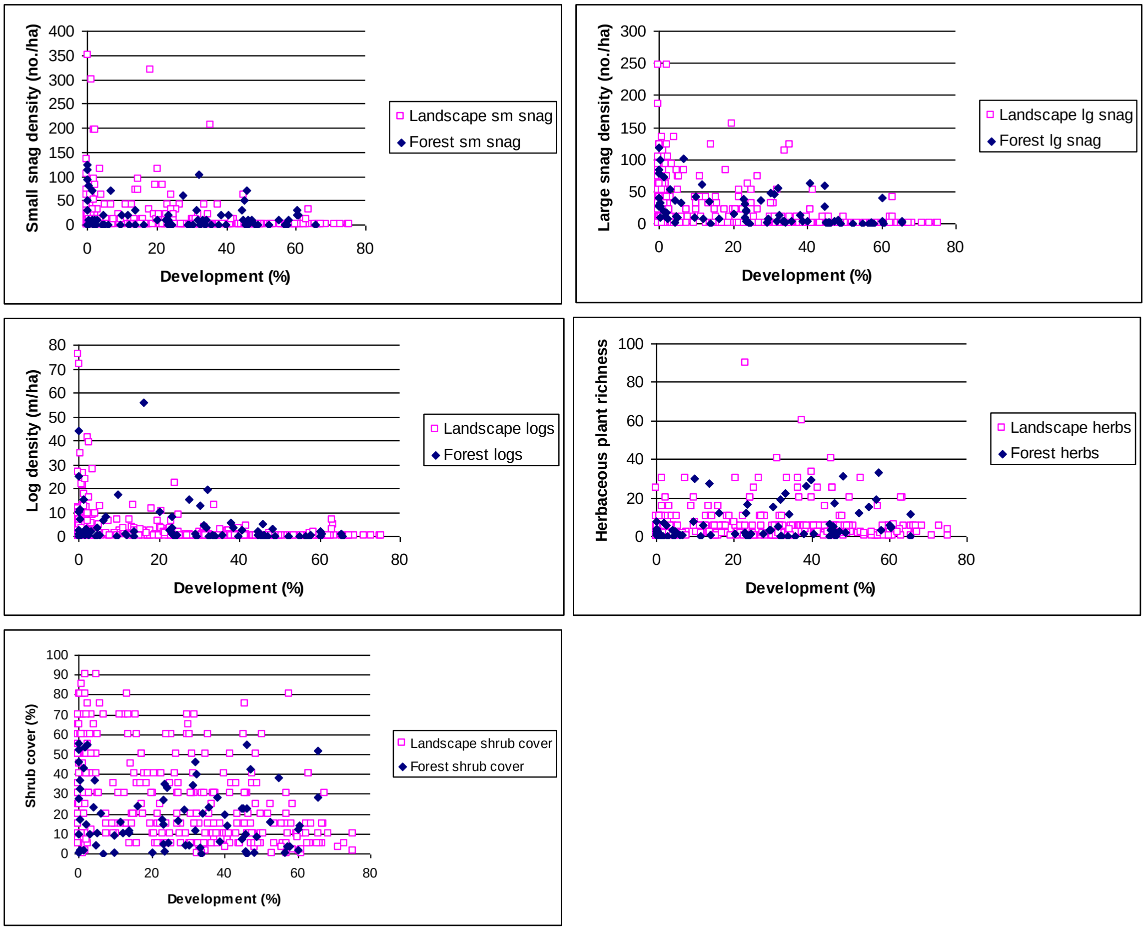


Figure 6.10. Scatter plots showing the relationships between dead wood and understory plant characteristics and development for two types of sites: native forests and throughout the landscape. Data were collected at 375 sites below 2100 m in elevation in the Lake Tahoe basin in 2003-2005.

Community Ordination and Variance Partitioning

In the CCA with all variables, ordination axis 1 was highly correlated with wetness (r = -0.85), no-snow date (r = -0.81), and easting (r = 0.75); axis 2 was correlated with slope (r = 0.60) and aspect (r = 0.56) (Figure 6.11). These patterns largely reflect the strong precipitation gradient across the basin, with the west sites having high wetness, late snow-melt date (due to the general east-facing aspect and shading by dense fir forests), and high precipitation, while the east basin has low precipitation and high heat load index (due to the general west-facing aspect and open Jeffery pine forests). Development, impervious surfaces, number of people and dogs per hour were somewhat correlated with easting, since sites in the east part of the basin were more developed than in the west basin.

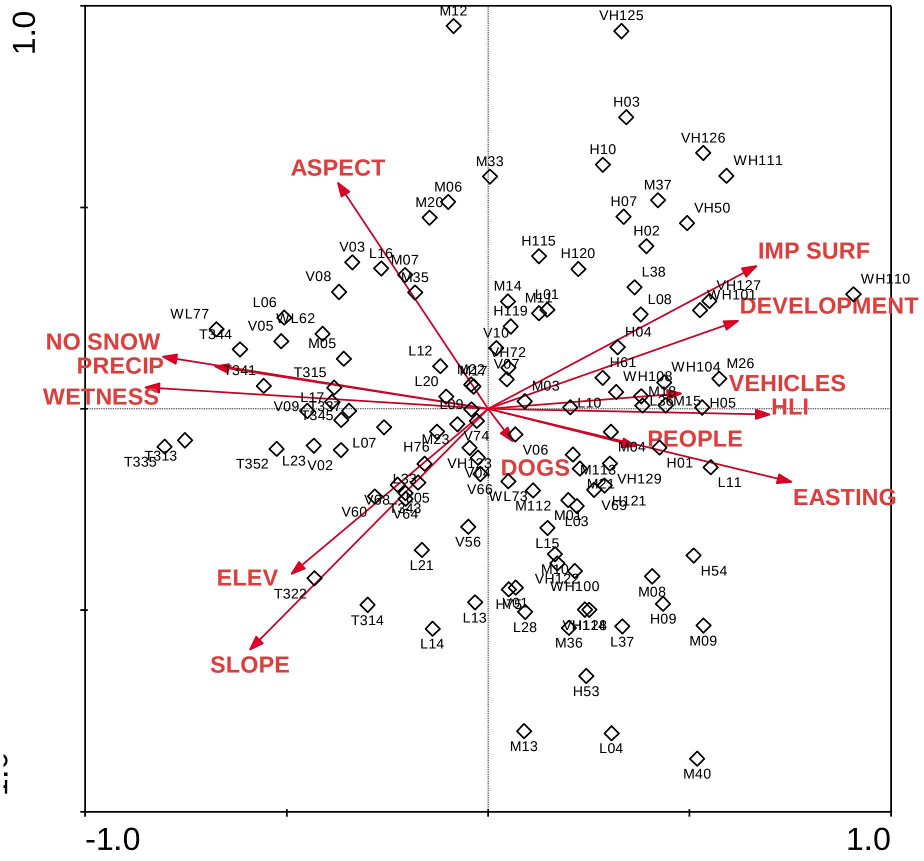


Figure 6.11. Biplot of sites with environmental variables: snow-melt date (no-snow), GIS-modeled average annual precipitation (precip), GIS-modeled soil moisture (wetness), GIS-modeled elevation (elev), GIS-modeled slope (slope), GIS-modeled aspect (aspect), GIS-modeled heat load index (HLI), easting, number of dogs per hour (dogs), number of people per hour (people), number of vehicles per hour (vehicles), , development within 300 m (development), impervious surfaces within 300 m (imp surf).

In E|H, axes 1 and 2 explained 8.8% of the total variation in the dataset (Table 6.3). Axis 1 was most strongly correlated with wetness (r = -0.764), no snow (r = -0.76), and easting (r = 0.71), while axis 2 was highly correlated with slope (r = -0.90). In H|E, axis 1 was correlated with impervious surfaces (r = 0.73), and axis 2 was correlated with development (r = -0.71) and people per hour (r = -0.66). However, neither canonical axis 1 nor all axes together were significant (Table 6.3).

Table 6.3. Summary of axes for CCA of (a) E|H, and (b) H|E.

(a)

Axis	1	2	3	4	All axes
Eigenvalues	0.274	0.165	0.103	0.073	
Cum. Percentage variance of species data	5.5	8.8	10.9	12.4	
Monte-Carlo test P-value	0.002				0.002

(b)

Axis	1	2	3	4	All axes
Eigenvalues	0.105	0.074	0.038	0.03	
Cum. Percentage variance of species data	2.3	4.0	4.9	5.5	
Monte-Carlo test P-value	0.082				0.084

Environmental variables explained more of the variation (14%) than human-caused variables (5%), but most of the variance was unexplained (77%) (Figure 6.12). Only 4% of the data could be attributed to either E or H, suggesting little overlap in their effects. Partitioning of the dataset with all species gave similar results, but had a slightly higher percentage of unexplained variance (82%), suggesting that inclusion of rare species did not contribute to a better understanding of the data.

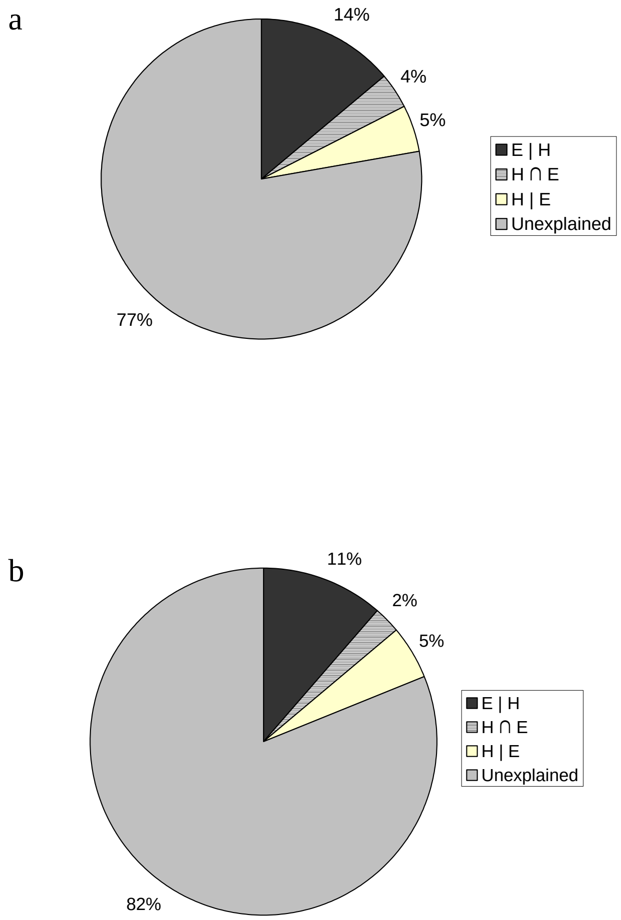


Figure 6.12 Variance partitioning for common species (a) and all species (b). “E” is naturally occurring environmental variables and “H” is human-caused variables.

Discussion

Native vegetation was not greatly altered in response to increasing surrounding development. In native forests, surrounding urban development had no impact on tree species composition, density, basal area, or number of canopy layers. The Tahoe Basin is a tourist destination primarily valued for its natural beauty and outdoor recreation opportunities (Nechodom et al. 2000). In keeping with this theme, the majority of private property owners have allowed native vegetation to persist in a somewhat natural state, planting only the occasional garden or ornamental tree.

Total species richness increased slightly with development, primarily due to increased numbers of exotic annual and perennial herb and grass species. Exotic species were present along the entire development gradient, including one site with 0% urban development within 300 m. This pattern met expectations of increasing exotic species with increasing development, and suggests that urban lots are susceptible to invasion by exotic species. Urban areas were more susceptible to invasion by exotic species, reconfirming previous studies. Some of the exotic species, such as *Bromus tectorum*, *Dactylus glomerata*, *Taraxicum officinale*, *Elytrigia pontina*, *Lotus corniculatus* should be of particular concern to land managers because of their abundance and/or invasiveness.

Exotic species have recently become recognized as a significant conservation concern, as they have been shown to replace native species and may alter ecosystem function (Vitousek 1986). Invasion in urban areas may be caused by increased availability of suitable microsites due to soil disturbances and/or trampling of dominant vegetation to create openings, or increased input of nutrients such as nitrogen and phosphorus (Hobbs and Heunneke 1992). In the Tahoe Basin, exotic species were most likely introduced via foot traffic and vehicles. However, these species were of little importance to the plant community in terms of relative percent cover (Figure 6.4). Growth and reproduction of exotic species may be limited by the cool, dry montane environment.

Urban development did not appear to impact percent cover of native annual herbs, perennial herbs, and shrubs. However, the slight decline in average percent cover of native trees suggests that urban sites have more open canopies. Native perennial grasses increased in both richness and average percent cover with development, suggesting that they are better adapted to the stresses of urban environments. The more open canopy and high heat load index (not discussed here in detail) found in urban sites may give perennial grasses a competitive advantage.

Urban development did not appear to have an impact on tree species composition, density or basal area per hectare. The diversity of height classes occupied by vegetation was not correlated with development. Conversely, in the larger landscape did show a decline in small and medium diameter trees with greater development, indicating that native forests retain important habitat elements, in this case vertical diversity of vegetation, that would otherwise be rarely occurring in a developed landscape.

Decadence features showed no obvious correlations with environmental factors. Contrary to expectations, disease symptoms were not more common in highly urbanized areas, and features associated with older trees (such as large cavities or broken tops) were not more prevalent in remote sites. However, light foliar color, oozing sap, and leaf necroses were ubiquitous, witnessed on all conifer species throughout the low elevations of the basin. Logging in the Tahoe Basin has been shown to increase dwarf mistletoe infections on Jeffery pine (Maloney 2000), and fire suppression has been shown to increase tree density, accumulation of dead wood, insect and pathogen outbreaks, and vulnerability to catastrophic fires (Elliot-Fisk et al. 1996, Ferrell 1996, Maloney and Rizzo 2002). Dwarf mistletoe infections, on Jeffery pine, are significantly higher in logged stands than unlogged stands in the Tahoe Basin (Maloney 2000). Therefore, low-elevation seral stands are all likely to be heavily diseased, regardless of urbanization status.

Urban development was strongly associated with the loss of woody debris from the ecosystem, both within remaining native forests and the landscape-at-large. Snag density, snag volume, and volume of coarse woody debris were negatively correlated with development, while number of cut stumps was positively correlated. Average snag decay class declines with development, suggesting that only newly dead snags remain in urban areas. In addition, while remote sites varied greatly in amount of dead wood, highly developed areas were consistently low.

Snags and logs are important elements of forest ecosystems; they provide essential habitat, nesting sites and feeding substrates for vertebrates (Bull 2002), invertebrates (Machmer 2002, Lindgren and MacIsaac 2002), bacteria and fungi (Zielonka and Piatek 2004). Decomposing logs also play a role in nutrient and carbon cycling (Zielonka and Piatek 2004). Asymbiotic nitrogen fixation in decaying logs, by nitrogen-fixing microbes, is likely an important contributor to the nitrogen cycle, particularly in places where atmospheric and symbiotic fixation is low (Brunner and Kimmins 2003). Decayed wood plays a role in maintaining soil structure by providing a long-term input of humus to the soil.

The properties of woody debris differ among decay classes (Harmon et al. 1986, Mori et al. 2004). Less-decayed wood does not provide a good growing substrate because of its hardness, low nutrient content, and low moisture content. Nor is highly-decayed wood a good growing substrate. As woody debris approaches the properties of soil, it loses height, leading to shading and burial by litter, and infection by pathogenic fungi increases. Consequently, intermediately-decayed woody debris provides the best growing substrate for seedling establishment (Mori et al. 2004). Therefore, it is important that an ecosystem have a regular supply of new dead wood, allowing for the continued availability of intermediately-decayed wood.

The Sierra Nevada, in general, has been subject to fire suppression for over a century, resulting in myriad ecological and human safety problems, such as altered forest structure, increased tree density, increased accumulation of dead wood, increased insect outbreaks, lowered biodiversity and vulnerability to catastrophic fires (Elliot-Fisk et al. 1996, Ferrell 1996). To combat these problems, local managers have taken an active role in reducing dead wood build-up, focusing efforts particularly on the urban-rural interface. Practices include timber harvest, prescribed burning, vegetation thinning, and creation of forest openings (Tahoe Regional Planning Agency 2004). In addition, activities by local residents, such as firewood collection, contribute to the loss of woody debris. Evidence of these practices was apparent from the low numbers of snags and logs and a high number of cut stumps in urban areas.

Chapter 7:

Human Use

Introduction

Disturbance within remnant forests in the form of human use and domestic animals often accompanies development in the surrounding area. The removal of snags for firewood, safety on roads and trails, and defensible space from wildfire are also common practices in undeveloped lands in proximity to urban environments. Fragmentation studies that ignore human disturbance risk confounding these two stresses because population- and community-level effects of recreation mirror those of small patch size and high patch isolation in many cases (Boyle and Samson 1985, Knight and Gutzwiller 1995, Riffell et al. 1996, Fernández-Juricic 2000a, Gutzwiller et al. 2002). Selective extinctions brought about by human presence may also lead to altered compositional patterns and community dynamics. We characterized use of sites by people and their pets to enable us to distinguish between effects associated with fragmentation and habitat loss from those associated with within-site disturbance, and to describe the nature of the relationship between surrounding development and within-site disturbance in the Lake Tahoe basin. Our goal is to characterize the types, intensity, and spatial and temporal distribution of anthropogenic disturbance at sample sites.

Methods

Field Data Collection

A 200 x 200-m sample unit (4 ha) was established in association with each sample point. Sampling for each species group occurred throughout areas of varying extents, but the majority of samples were taken within a 4-ha area around the sample point. In standard sample units, 4 ha encompassed the vegetation plots, ant grid, small mammal grid, center point count station, and center trackplate and camera stations. All satellite point count stations and most satellite trackplate and camera stations fell outside the 4-ha area.

Study sites for the LTUB project were subject to dispersed use with multiple access points. Under these conditions, personal observation is the most effective and unbiased sampling method available. Personal observation consisted of an observer moving through the study site and recording data on the type and intensity of use encountered. A total of approximately 1.2 km of survey routes and 5 count stations were established within the sample unit. Some sites were smaller than 200 x 200 m (defined by the extent of the undeveloped area), and at these sites transect lengths were reduced commensurate with the reduced size of the sites. At sites smaller than 1 ha, no transects were conducted; one or two 10-min counts were conducted instead.

Surveys were stratified by day of the week (weekday non-holiday, and weekend and holidays), time of the day (dawn to mid-day, mid-day to evening), and month (May through September) (Table 7.1). Each study site was surveyed once per week, with one survey allocated to each combination of time of day and segment of week over a four-week period. Observers rotated among sites so that any observer bias that might exist was represented equivalently among study sites. The order in which sites were surveyed within a time slot was rotated.

Table 7.1. Sampling strata used to partition survey effort to characterize anthropogenic stressors within sample sites.

Type of strata	Number of strata	Description of strata
Month	5	May through September
Segment of week	2	Weekday non-holiday and weekend/holiday
Time of day	2	Morning (dawn to 1300 hrs), afternoon (>1300 to dusk)

Data recorded included observer, date, survey start and end times, start and end locations, route completed, and weather. All encounters were recorded including location of detection with respect to the observer and to the sample unit. Other information regarding encounters included

- type of use (truck, ATV, walking, running, bicycle, stationary, etc);
- if stationary, then type of activity (picnic, sitting);
- number of people in group;
- presence of non-vehicular noise (shouting, music, machinery);
- type and number of domestic animals (restrained/unrestrained); and
- other activities (feeding animals, littering, on/off trail use).

In the course of conducting the walking survey observers stopped at designated points for 3 minutes and recorded all encounters during that time. The distance to detections was recorded, as well as the location inside or outside the sample unit. Counts provided data on the density of use by type, whereas transect data provided frequency of use by type. Observers had the option of conducting a 30-sec traffic count at each count station, if they determined that recording traffic during a 3-min count would be distracting. The 30-sec counts consisted of observers tallying all vehicles at all distances in 30 sec either before or after the 3-min count. At a later date, the frequency and density of use by type will be summarized by segment of day and segment of week for each site.

Data Analysis

The frequency by use type (encounters along transect) and intensity (number and density of detections during counts) of use was summarized by month, per time of day, and for the spring/summer season as a whole. We calculated four variables to describe the use of each site by people, all dogs, unrestrained dogs, and vehicles. We combined data from transects and counts for all analyses. We calculated the total number of people (e.g., walking, running, biking, golfing, standing), total number of dogs, and number of unrestrained dogs detected per hour within the sample unit based on the total number of detections across all visits multiplied by 60 and divided by the total survey time per site.

We also calculated an index of traffic surrounding the sample unit to reflect traffic use and noise around the sample unit. Vehicle tallies consisted of transects, 3-min counts, and in some cases 30-sec counts. If there was a 30-sec count conducted at a particular count station at a particular visit, we multiplied the count by 6 (to arrive at a 3-min estimate) and superseded the number of vehicles detected during the 3-min count. All non-vehicle detections during the 3-min count were retained for other calculations; the 30-sec count could only supersede the vehicle totals for counts. The resulting value for 3-min/30-sec counts was summed across visits for each site and added to the number of vehicles detected during all transect surveys at each site. This value was multiplied by 60 and divided by the total survey time to yield the number of vehicles detected per hour.

We summarized the overall patterns of use in terms of the four use variables and performed simple linear regressions between these variables and development within 300 m.

Results

Survey Effort

We conducted 1,684 surveys of human use at 101 sites over a 6 month period and distributed between weekdays and weekends (Table 7.2), for a total survey time of 959.9 hr. The number of visits per site ranged from 12 to 21 ($\bar{x}$ = 16.7, s.e. = 0.16); the variation was a result of some sites being established and therefore survey efforts began earlier than others. Total survey time per site ranged from 2.33 to 17.03 hrs ($\bar{x}$ = 570.25, s.e. = 23.59), with the variation primarily a function of the size of the sites.

Table 7.2. Number of visits to 101 sites along an urban gradient in the Lake Tahoe basin in 2004 by month, time of day (early = 6 am to 1 pm, late = 1 pm to 8 pm), and time of week. "Weekends" include holidays (Memorial Day, Independence Day, and Labor Day).

	Weekdays		Weekends		
	Early	Late	Early	Late	Total
May	10	21	21	33	85
June	73	77	77	68	295
July	136	82	136	96	450
August	122	99	131	99	451
September	100	84	105	114	403
Total	441	363	470	410	1684

Use Patterns

The number of people detected per site ranged from 0 to 32.3 people/hr, including the most heavily used site, WH109N, which had nearly three times as many detections per hour as the next most used site. This small site, which had very high human use with relatively little survey effort, was a clear outlier and was omitted from site-specific analyses of detections of people, but retained for analyses of dogs and vehicles. With the outlier removed, the number of people detected per site ranged from 0 to 11.18 people/hour ($\bar{x}$ = 1.59, s.e. = 0.23). The total number of dogs detected per hour per site ranged from 0 to 4.5 ($\bar{x}$ = 0.37, s.e. = 0.07), and the number of unrestrained dogs per hour per site ranged from 0 to 2.33 ($\bar{x}$ = 0.24, s.e. = 0.04). The number of vehicles detected per hour per site ranged from 0 to 323.08 ($\bar{x}$ = 33.26, s.e. = 5.31).

Use by people varied depending on the month, time of day, and time of week. Use appeared to peak in July (Fig. 7.1), was somewhat heavier in the afternoon and evening than in the morning (Fig. 7.2), and was somewhat heavier on weekends and holidays than on weekdays (Fig. 7.3).

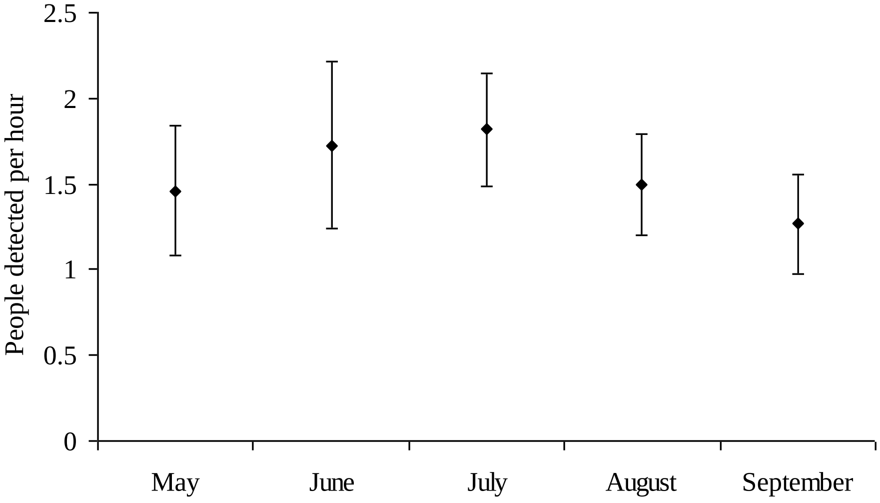


Figure 7.1. The number of people/hour in each of the five months surveyed at 101 sites along an urban gradient in the Lake Tahoe basin, 2004. Only 69 sites were surveyed in May and 99 were surveyed in June.

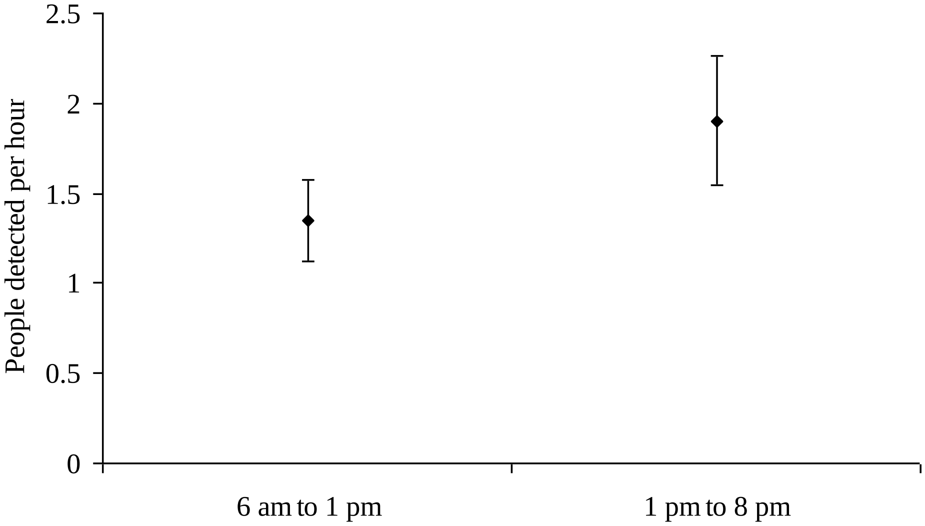


Figure 7.2. The number of people detected per hour in early (6 am to 1 pm) surveys and late (1 pm to 8 pm) surveys at 101 sites along an urban gradient in the Lake Tahoe basin, 2004.

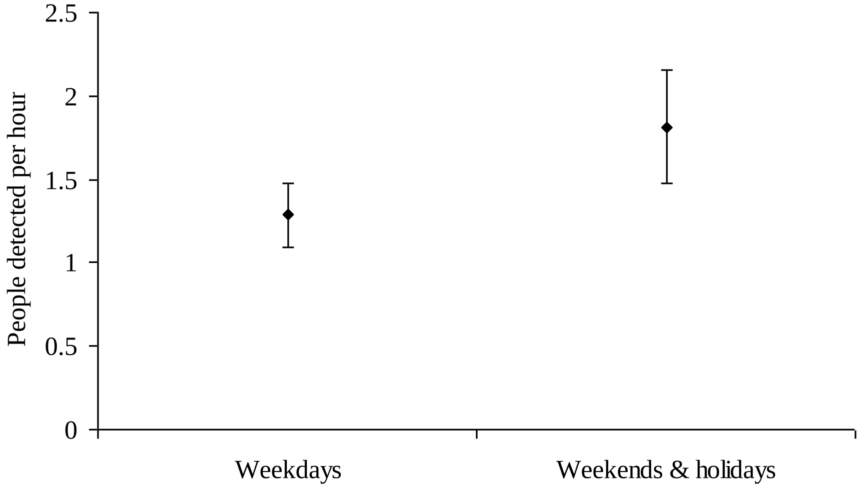


Figure 7.3. The number of people detected per hour on weekdays and on weekends and holidays (Memorial Day, Independence Day, and Labor Day) at 101 sites along an urban gradient in the Lake Tahoe basin, 2004.

Most dogs detected were not restrained. Of the 315 dogs detected within sample units across the entire study, 226 (72%) of them were unrestrained. In the 58 sites where dogs were detected, the proportion of dogs unrestrained (as measured by the number of unrestrained dogs detected per hour divided by the total number of dogs detected per hour) ranged from 0 to 1 ($\bar{x}$ = 0.67, s.e. = 0.05).

Human use was positively related to development within 300 m of the site center (F(1,98) = 12.31, $P = 0.0007$, adj. $R^2 = 0.10$; Fig. 7.4), while the number of vehicles showed a an even stronger positive relationship with 300-m development (F(1,99) = 36.30, $P < 0.0001$, adj. $R^2 = 0.26$; Fig. 7.5). The total number of dogs was marginally positively related to development (F(1,99) = 3.52, $P = 0.0636$, adj. $R^2 = 0.02$), but not the number of unrestrained dogs (F(1,99) = 1.37, $P = 0.2451$, adj. $R^2 = 0.00$). Dogs were more likely to be restrained in more developed areas (F(1,56) = 6.89, $P = 0.0112$, adj. $R^2 = 0.09$; Fig. 7.6).

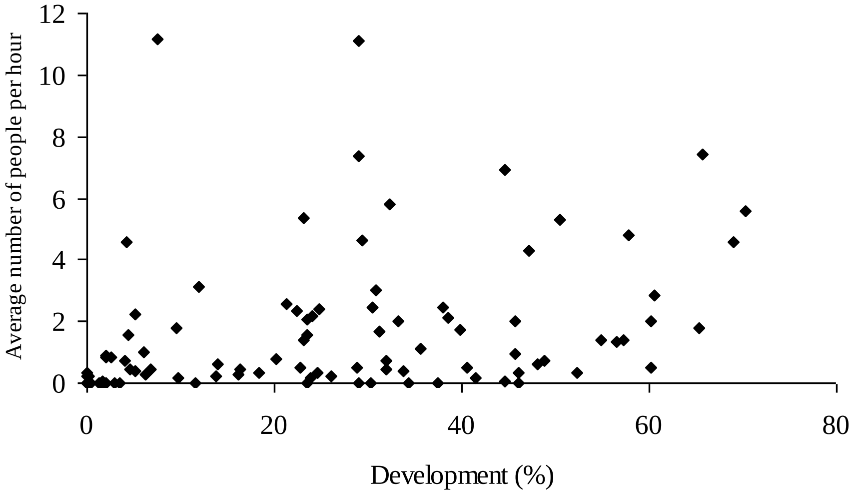


Figure 7.4. Relationship between the number of people detected per hour and development within 300 m of 100 sample units in the Lake Tahoe basin, 2004.

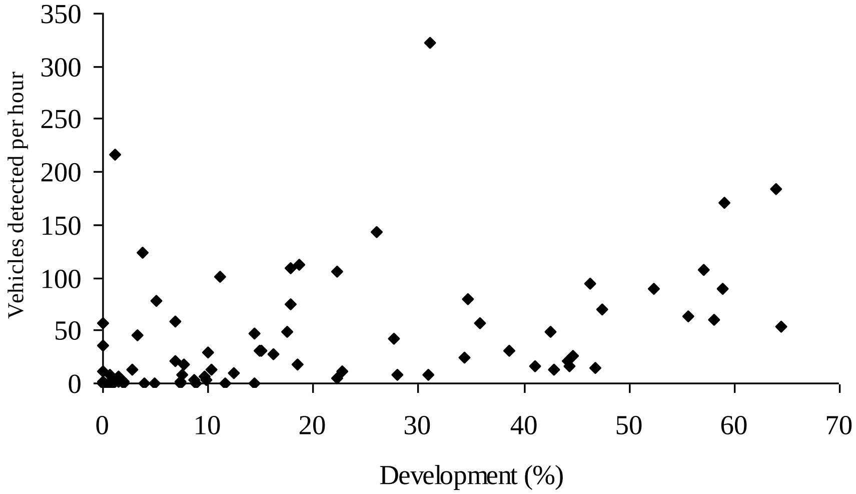


Figure 7.5. Relationship between the number of vehicles detected per hour and development within 300 m of 101 sample units in the Lake Tahoe basin, 2004.

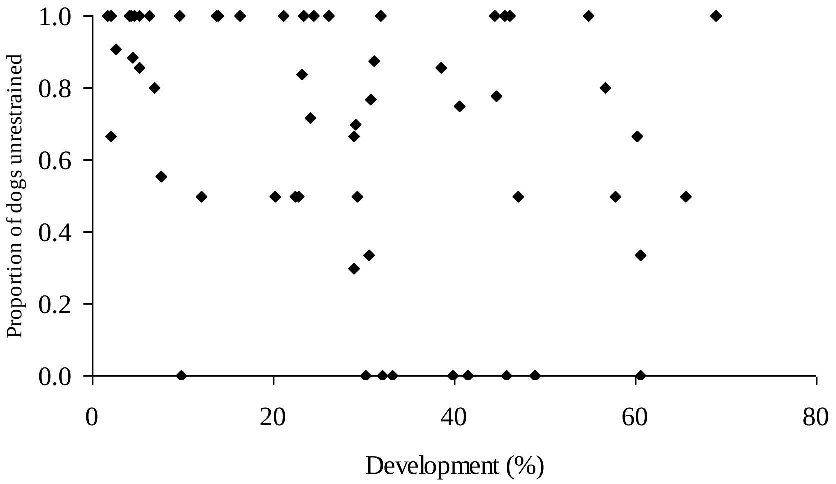


Figure 7.6. Relationship between the proportion of dogs unrestrained (off leash) and development within 300 m of 101 sample units in the Lake Tahoe basin, 2004.

Discussion

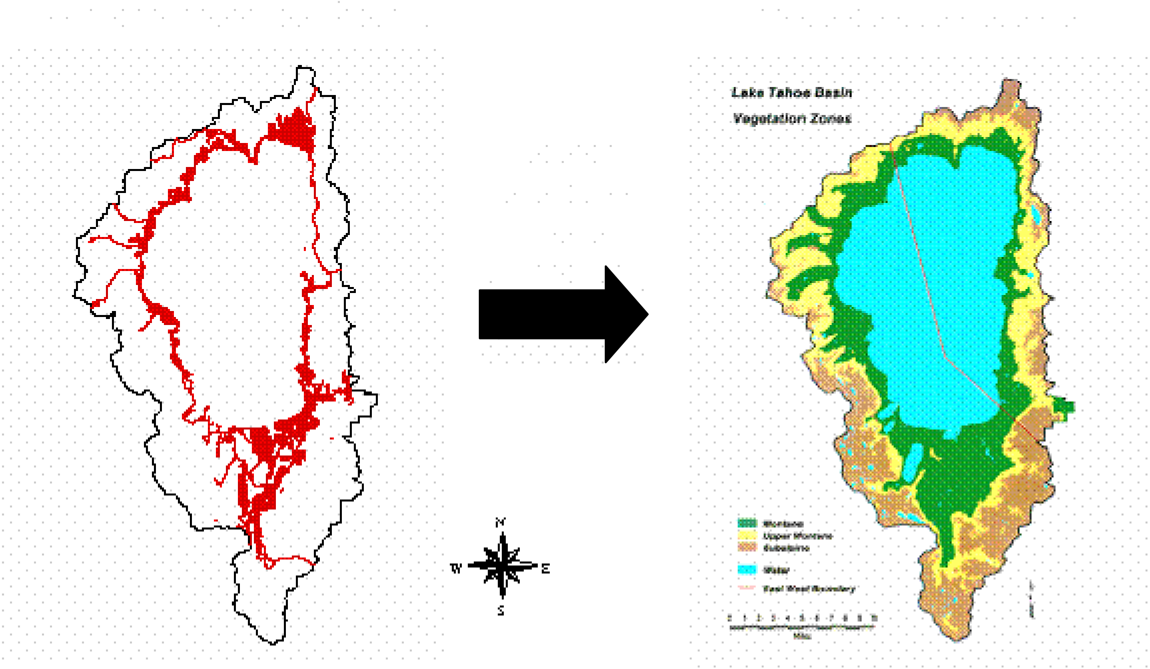
Although recreation use was positively related to development, it was clear that some sites with low development received high use, particularly non-motorized use. This means that use can have an impact independent of development and that analyses of development should not assume that forms of human disturbance increase with development in a linear manner. Further, it appears that some types of impacts from dogs (e.g., wildlife harassment and mortality) may be greater in less developed areas because a greater proportion of dogs are unrestrained.

As expected, peak use months were June, July and August, and a greater number of people on the weekends. This indicates that summer visitors comprise a large proportion of users of these urban forest parcels, which is perhaps a new perspective on how many visitors spend their time and what aspects of land management in the basin will affect visitor satisfaction. The greater level of use in the latter portion of the day is consistent with the idea that most people go for walks with or without pets toward the end of the day.

Chapter 8:
Landscape Model

Introduction

As part of the research project investigating the role of urban forests in maintaining biological diversity in the Lake Tahoe basin, we built spatially explicit models of basin-wide conditions for species and species groups sensitive to development. The models were based on data generated through field data collection, and then used to make predictions about ability of sites and landscapes to support species and assemblages. The model applies to the lower montane vegetation zone (< 7000 ft), which is where the majority of development and human use has occurred (Fig. 8.1). The lower elevation vegetation is predominantly Jeffrey pine and mixed conifer forests.



Impervious surfaces **Vegetation zones**

Figure 8.1. Coincidence of development and vegetation zones in the Lake Tahoe basin, illustrating that most of the development is occurring in the lower elevation vegetation zones.

The goal of GIS modeling was to make predictions about the presence or abundance of species or species groups throughout the lower montane zone (below 7000 ft) to inform our understanding of the current and potential future amount and location of high quality areas for species sensitive to human development.

Methods

Regression Model Development

We selected the response variables with the strongest relationship with development or GIS variables that we observed to vary with development, namely NDVI and canopy cover. Ten models were developed across the taxonomic groups based on the strength of relationships:

- bird species richness
- bird community dominance
- ground-nester richness
- cavity-nester richness
- small mammal species richness
- small mammal abundance
- black bear presence
- marten presence
- coyote presence
- ant species richness
- log-nesting ant richness
- thatch-nesting ant richness
- *Camponotus modoc* abundance
- *Formica micropthalma* abundance
- *Formica ravida* abundance
- Exotic plant species richness

We used all possible subsets regression to derive the best predictive model for each response variable. Explanatory variables were limited to GIS variables to enable us to make predictions throughout the basin. For each response variable for each taxonomic group, we identified the GIS variables that had the potential to affect the response variable given our ecological knowledge of the system. As with the regression modeling in the taxa-specicfic chapters, data for many of the habitat variables were available at multiple spatial scales (e.g., landscape vegetation at 100, 300 and 1000 m). We used AICc values to help identify the most appropriate scale at which to describe features for which multiple scales were an option. The spatial scale to include in the GIS models was determined by the model with the highest rank (greatest model weight).

After selecting the predictor variables to use in the models, we looked for potential interactions among these variables. A generalized additive modeling (GAM) procedure based on nonparametric regression and smoothing techniques was used, which can uncover structure in the relationship between the independent variables and the dependent variable that might otherwise be missed. GAM was conducted using Program R (R Development Core Team 2005).

The all possible subsets regression was conducted using PROC LOGISTIC adjusted for species detectability for presence/absence response variables, and for continuous variables we conducted all possible subsets regression using PROC REG and then used PROC GLIMMIX to calculate AICc values and relative weights. The maximum number of variables considered for inclusion in the all possible subsets regression was limited to 10% of the number of sites sampled to avoid overfitting. For each number of variables (ranging from 1 to the max number included in the analysis), we identified the 10 models with the lowest AIC as candidate models. For example, if 6 predictor variables were included in the analysis, 60 candidate models would be selected. We used model averaging to derive the final predictive model.

For continuous variables, PROC GLIMMIX can account for count data (all richness and abundance data), but only PROC REG can do all possible subsets regression. Thus, we used a two step analysis process for count data. Continuous, response variables were log transformed prior to the all possible subset analysis in PROC REG so that the AICc values among competing models most closely aligned with what the AIC values would be in the final step of the analysis conducted in PROC GLIMMIX. The best 10 models in each number of variables were carried forward into PROC GLIMMIX where their relative AIC values were calculated and weights assigned. Predictor variables for birds and small mammals were standardized prior to the analysis by subtracting the mean and dividing by the standard deviation.

GIS Model Development

Development Scenarios

Multiple development scenarios were modeled to demonstrate the magnitude of the contribution that public parcels make to supporting biodiversity and to represent potential future development options. We partitioned parcels into three categories: private vacant (currently undeveloped), Forest Service urban parcels, and all public urban parcels. This categorization allowed us to model likely future development trends on private lands, as well as to evaluate changes that would result if the same trends occurred on public urban lands. Although it is not currently likely that public parcels will be converted to private ownership on a large scale, nonetheless we modeled development of public urban parcels to quantify the contribution they make to supporting biological diversity in the lower montane zone (or more correctly, the contribution that would be lost if developed).

We thought it was most likely that single family homes would be built on private parcels. We calculated current coverage of developed parcels zones as single family home, and found the average coverage to be 51%. Therefore, we represented parcel development by randomly assigning development to 50% of the parcel acreage. We also wanted to represent lower intensity uses, such as the establishment of trails and public service uses (e.g., sediment ponds). We represented these types of uses on public lands by randomly assigning development to 10% of the parcel.

We modeled and compared five development scenarios for this report; they are listed in order of increasing extent of development.

1. Existing conditions
2. Half of all private vacant parcels developed
    - There are currently 6110 undeveloped private parcels in the basin; so 3055 parcels were randomly selected and represented as having a simple family home (50% developed).
3. All private vacant parcels developed as above
    - All 6110 parcels were represented as having a single family home (50% developed).
4. All private vacant parcels developed as above and all public urban parcels developed for some public service
    - There are 8348 public urban parcels – they were all represented as 10% developed.
5. All private vacant parcels developed as above and all Forest Service urban parcels developed
    - There are 3318 Forest Service urban parcels – they were all represented as 50% developed.

<u>Parcel Identification</u>

The base landuse layer for all management scenarios was the combined parcel layer created in c. 2000 by TRPA (ltb_landuse_u10.shp). However, this layer did not have all the information needed to run the management scenarios (it had landuse but not ownership). Ownership was determined by consulting parcel layers provided by individual agencies. We obtained a parcel layer named "CTC_parcels.shp" from the California Tahoe Conservancy (Scott Cecchi pers. comm.). We also obtained a parcel ownership layer (parcels06142006_nad27.shp) from the LTBMU (Kurt Teuber pers. comm.), which was used to identify Burton-Santini parcels and private vacant parcels.

In the LTBMU layer, there were 3,332 National Forest System (NFS) Burton-Santini (B-S) parcels in the basin. Mismatches between the base landuse layer and the LTBMU layer resulted in a slight decrease in the final number of parcels represented as B-S to 3,327. Of these parcels, only those with centroids $\leq$ 7000 ft (n = 2,711) and those few parcels with centroids above 7000 ft but $\leq$ 50 ha in size (n = 607) were considered eligible for development under our scenarios, for a total of 3318 parcels. This "weeding" was performed to exclude the few large, high elevation parcels (n = 9) that are unlikely to be developed.

The other public lands in urban areas in the basin span multiple agencies, including California Tahoe Conservancy (CTC), Nevada State Lands, and county lands. In CTC layer there were 4,542 parcels owned by CTC or that have a CTC easement. Mismatches between the base landuse layer and the CTC layer slightly reduced the final number of parcels represented as CTC land to 4,384. A number of other public agencies own and manage urban parcels in the basin, such as the State of Nevada and counties. Nevada owned parcels were selected in the LTBMU parcel layer by selecting "Owner = "State", "State = NV" and "GenUse = Vac" (n = 485). County owned parcels were identified using the LTBMU parcel layer by selecting "Owner =

County" and "GenUse = Vac" (n = 170). As with forest Service parcels, only those occurring $\leq$ 7000 ft or above 7000 ft and $\leq$ 50 ha were eligible for development. The final selection of parcels on the landuse layer was performed as previously described and resulted in 478 Nevada-owned parcels and 168 county-owned parcels. This approach resulted in a total of 5030 public urban parcels other than NFS B-S parcels.

In the LTBMU parcel layer, private parcels were identify by selecting all parcels labeled as "Owner = Private" and "Landuse = 1" (n = 6116). Next, all parcels in the landuse layer that had their center in these 6,116 selected parcels were labeled with the 'Private-vacant' label in the "scenario" field. The final number of private vacant parcels represented in the landuse layer was slightly reduced to 6,110.

Development Representation

Development was allocated to parcels by randomly selecting 3x3 m pixels within each parcel until 10 or 50% of the pixels are selected. In addition to changing pixel classification from undeveloped to developed, we also considered that other GIS variables are likely to change with development, such as tree density and canopy cover. We evaluated correlations among variables that could change with development that were available in GIS: NDVI, (Normalized Difference Vegetation Index), brightness and canopy cover. We created a series of points 300 meters apart, and extracted the values of these three variables within a 300 m radius. We only used points with a development value of $\geq$ 1% in the analysis. Based on linear regression analysis, we found that only two variables were significantly associated with development: NDVI and canopy cover (Table 8.1). Although the relationships had a lot of variability, intuitively it was important to account for related changes, and the slope of the relationship with canopy cover was steep, indicating a high magnitude of change in canopy cover with development.

Table 8.1. Regression relationships between development ($\geq$ 1%) and three variables that commonly change as a result of development.

Variable	**Adj. R^2**	**Slope**
NDVI	0.072	-0.0013
Brightness	0	0
Canopy cover	0.092	-0.219

To represent these relationships in the scenarios, we first altered our development values for each scenario, as described above. We then subtracted the current development values from the development value in each scenario, giving us a net change (positive or negative) in development value for each pixel, and then we calculated the associated change in NDVI and canopy cover based on the regression equation. We finally added together two layers (the net change in NDVI and canopy cover and the original NDVI and canopy cover used in various landscape models) to derive the altered values.

Bird Modeling

A total of 32 predictor variables were included for consideration in all-possible-subsets modeling (Table 8.2) although this number varied slightly by response variable. In addition to these linear terms, quadratic terms were also included for six of these variables, for a total of 38 variables.

Some variables were transformed to reduce the influence of outliers or yield a linear relationship with the response variable. We found no significant interactions among these predictor variables based on GAM analyses. Models up to 15 variables were allowed; the high number relative to that of the other taxonomic groups reflects the large number of sample points (n = 375) with bird data. By and large, models did not improve with >15 variables included. The best 10 models for each number of variables, for a total of 150 models, were retained for use in model averaging.

Table 8.2. Variables included in regression models for predicting bird species richness, bird community dominance, ground nester richness, and cavity-nester richness.

Variable	**Definition**
dev150	Development within 150 m
dev300	Development within 300 m
dev500	Development within 500 m
dev1000	Development within 1000 m
as150	Proportion aspen within 150 m
as300	Proportion aspen within 300 m
as500rt	Proportion aspen within 500 m (sqrt)
as1000	Proportion aspen within 150 m
hc150	Proportion high conifer (LPN, RFR, SCN, SMC) within 150 m
hc300	Proportion high conifer (LPN, RFR, SCN, SMC) within 300 m
hc500	Proportion high conifer (LPN, RFR, SCN, SMC) within 500 m
hc1000	Proportion high conifer (LPN, RFR, SCN, SMC) within 1000 m
hc10002	Proportion high conifer (LPN, RFR, SCN, SMC) within 1000 m (squared)
lc150	Proportion low conifer (JPN, WFR) within 150 m
lc300	Proportion low conifer (JPN, WFR) within 300 m
lc500	Proportion low conifer (JPN, WFR) within 500 m
lc1000	Proportion low conifer (JPN, WFR) within 1000 m
rm150rt	Proportion riparian-meadow (MRI, PGS, WTM) within 150 m (sqrt)
rm300rt	Proportion riparian-meadow (MRI, PGS, WTM) within 300 m (sqrt)
rm500rt	Proportion riparian-meadow (MRI, PGS, WTM) within 500 m (sqrt)
rm1000rt	Proportion riparian-meadow (MRI, PGS, WTM) within 1000 m (sqrt)
sh150rt	Proportion shrubs (MCP, SGB) within 150 m (sqrt)
sh300	Proportion shrubs (MCP, SGB) within 300 m
sh500	Proportion shrubs (MCP, SGB) within 500 m
sh1000rt	Proportion shrubs (MCP, SGB) within 1000 m (sqrt)
elev	Average elevation within 3 x 3 cell grid in m
elev2	Average elevation within 3 x 3 cell grid in m (squared)
Slope	Average percent slope within 100 m
Slope2	Average percent slope within 100 m (squared)
DistWtr	Minimum distance in m to stream or lake
DistWtr2	Minimum distance in m to stream or lake (squared)
UTM_N	UTM N, zone 10
UTM_N2	UTM N, zone 10 (squared)
UTM_E	UTM E, zone 10
CC100	Canopy cover within 100 m
CC1002	Canopy cover within 100 m (squared)
ndvi	Average NDVI within 100 m
bright	Average brightness within 100 m

Carnivore Modeling

Thirty-one predictor variables representing development, local and landscape vegetation composition and structure and abiotic conditions, were included in all the all possible subsets regression analyses of carnivore occurrence (Table 8.3). Evaluation in GAM indicated no significant interactions among variables. The maximum number of variables in any single model was limited to 8 variables.

Table 8.3. GIS variables used in all possible subsets modeling process for carnivore occurrence.

Variable	Description
ELEV	Average elevation (feet) within a 45m radius
SLOPE_3X3	Average slope (degrees) within a 45m radius
PPT_MM	Precipitation (30 year average; 1971 - 2000), in mm
NDVI_3X3	Average NDVI within a 45m radius
BRI_3X3	Average brightmess within a 45m radius.
GRE_3X3	Average greenness within a 45m radius.
WET_3X3	Average wetness within a 45m radius.
DIST_STRM	Distance, in meters, to the nearest stream
DEV_100M	Proportion of the area within a 100 meter buffer that is "developed"
DEV_300M	Proportion of the area within a 300 meter buffer that is "developed"
DEV_500M	Proportion of the area within a 500 meter buffer that is "developed"
DEV_1000M	Proportion of the area within a 1000 meter buffer that is "developed"
DEV_MAX	Maximum value from 100, 300, 500, or 1000 meter scales
BAR_300	Proportion of the area within a 300 meter buffer that is CWHR type "BAR"
FOR_300	Proportion of the area within a 300 meter buffer that is forested (CWHR types JPN, LPN, RFR, SCN, SMC, WFR)
MDW_300	Proportion of the area within a 300 meter buffer that is meadow (CWHR types ASP, MRI, PGS, WTM)
SHR_300	Proportion of the area within a 300 meter buffer that is shrub (CWHR types MCH, MCP, SGB)
N34SP_300	Percent of area within 300 meter distance with trees 15 – 61 cm dbh and canopy cover < 40%
N34MD_300	Percent of area within 300 meter distance with trees 15 – 61 cm dbh and canopy cover > 40%
N56SP_300	Percent of area within 300 meter distance with trees > 61 cm dbh and canopy cover < 40%
N56MD_300	Percent of area within 300 meter distance with trees > 61 cm dbh and canopy cover > 40%
BAR_1K	Proportion of the area within a 1000 meter buffer that is CWHR type "BAR"
FOR_1K	Proportion of the area within a 1000 meter buffer that is forested (CWHR types JPN, LPN, RFR, SCN, SMC, WFR)
MDW_1K	Proportion of the area within a 1000 meter buffer that is meadow (CWHR types ASP, MRI, PGS, WTM)
SHR_1K	Proportion of the area within a 1000 meter buffer that is shrub (CWHR types MCH, MCP, SGB)
N34SP_1K	Percent of area within 1000 meter distance with trees 15 – 61 cm dbh and canopy cover < 40%
N34MD_1K	Percent of area within 1000 meter distance with trees 15 – 61 cm dbh and canopy cover > 40%

N56SP_1K	Percent of area within 1000 meter distance with trees > 61 cm dbh and canopy cover < 40%
N56MD_1K	Percent of area within 1000 meter distance with trees > 61 cm dbh and canopy cover > 40%

Small Mammal Modeling

Fourteen predictor variables were included in the all possible subsets regression analysis for small mammals (Table 8.4). We found no significant interactions among these predictor variables based on GAM analysis. For small mammal species richness, the maximum number of variables to include in a model at once was limited to seven due to sample size considerations. For small mammal total relative abundance, five was the maximum number of variables in a single model.

Table 8.4 GIS variables used in the all possible subsets modeling process for small mammal species richness and total relative abundance.

Variable	**Definition**
NDVI	Average NDVI within 100 m
Bri	Average brightness within 100 m
CF500	% cover of conifer forest (JPN, LPN, RFFR, SCN, SMC, WFR) within 500 m
SH500	% cover of shrubs (MCP, SGB) within 500 m
GR500	% cover of grassland (PGS) within 500 m
MERI_500	% cover of riparian (MRI/WTM) within 500 m
ASP_500	% cover of aspen (ASP) within 500 m
TR12-24	Trees 12-23.9cm DBH within 500 m
TR24_500	Trees >24cm DBH within 500 m
CANmd500	Moderate & dense tree density within 500 m
D100	Development within 100 m
D500	Development within 500 m
D1000	Development within 1000 m
D1000sq	Development within 1000 m squared

Ant Modeling

We conducted all possible subsets regressions for six ant community responses: ant species richness, abundance of log-nesters, abundance of thatch-nesters, abundance of *Camponotus modoc*, *Formica microphthalma*, and *Formica ravida*. We incorporated ten GIS-derived predictor variables (Table 8.5) in each of the regression models for ant community responses. We limited the maximum number of variables to seven for inclusion in each of the final models to prevent problems associated with the number of appropriate parameters in a given sample size (Burnham and Anderson 2002).

Table 8.5. GIS variables used in all possible subsets regression models for ant community responses.

Variable	Definition
HLI	Average heat load index of a 9-cell window around the site.
PPTmm	Precipitation (mm) of site based on 30-year mean from 1971-2000).
ASP	Aspect majority value of a 9-cell window.
NDVI	Average ndvi of a 9-cell window
GRE	Average greenness of a 9-cell window.
IMP100	Impervious surface area within 100 m .
DEV60	Average development value of a 9-cell window.
DEV1000	Average development value within a 1000-m buffer.
JPN100	Proportion of area within a 100-m buffer as Jeffrey Pine (JPN).
CC100	Average canopy cover within a 100-m buffer.

Plant Modeling

** in progress

Results

Bird Models

Species richness

The final model for species richness retained 28 variables, with strong influences of UTM N, elevation, percent development at several scales, NDVI, percent slope, brightness, and low and high conifer forest (Appendix 8.1). Because the management scenarios alter both development and NDVI, the scenarios had strong effects on species richness.

Predicted richness values across the landscape were placed into three categories based on one standard deviation above and below the mean predicted richness value (rounded off): high (≥ 20 species), moderate (14 to 20 species), and low (<14 species) richness. Increasing intensity of development increased the proportion of the landscape with low richness and decreased the proportion with moderate and high richness (Fig. 8.2). The proportion of the landscape with high richness ranged from 0.115 in Scenario 1, existing conditions, to 0.096 in Scenario 5. The proportion with low richness ranged from 0.139 in Scenario 1 to 0.199 in Scenario 5.

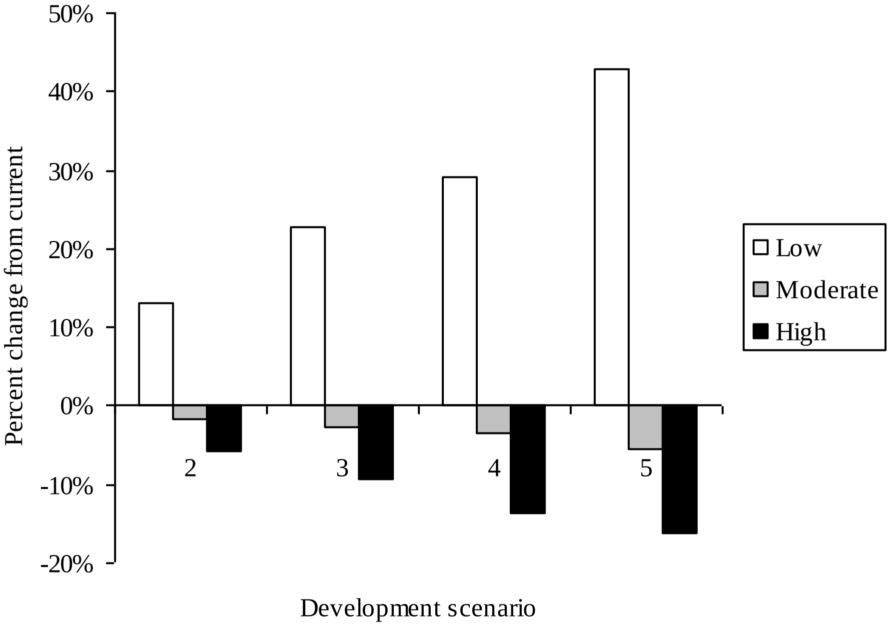


Figure 8.2. Predicted percent change in three categories of bird species richness in four development scenarios compared to existing conditions. High (≥ 20 species), moderate (14 to 20 species), and low (<14 species) richness.

Maps of model outputs show distinct changes in high- and low-richness areas in some portions of the basin (Map set 8.1). The most obvious area of change is in South Lake Tahoe, where high-richness areas in the Al Tahoe and Sierra Tract neighborhoods reduce in size or disappear completely. Likewise, high-richness areas east of Stateline decrease dramatically in size with increasing development, even in the least intense development scenario (Scenario 2). High-richness areas are also lost and/or reduced in size along the East Shore near Spooner Lake, and on the West Shore west of Rubicon Bay. Reductions in size of high-richness areas are accompanied by increases in size of low-richness areas in most cases.

Community dominance

The final model for community dominance retained 28 variables, with strong influences of NDVI, development at multiple scales, elevation, slope, distance to water, aspen, and low-elevation conifer forest (Appendix 8.1). Because the management scenarios alter both development and NDVI, the scenarios have strong effects on community dominance.

Dominance was placed into three categories based on one standard deviation above and below the mean predicted dominance value (rounded off): high (≥ 0.26), moderate (0.16 to 0.26), and low (<0.16). Increasing intensity of development decreased the proportion of the landscape with low and moderate dominance and increased the proportion with high dominance (Fig. 8.3). The proportion of the landscape with low dominance ranged from 0.129 in Scenario 1, existing conditions, to 0.109 in Scenario 5. The proportion with high dominance ranged from 0.133 in Scenario 1 to 0.200 in Scenario 5.

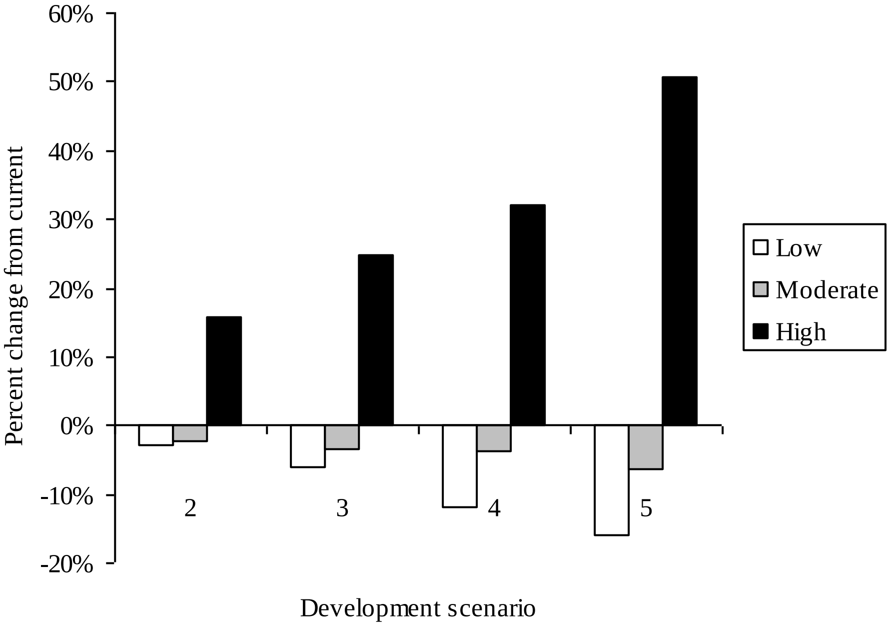


Figure 8.3. Predicted percent change in three categories of bird dominance in four development scenarios compared to existing conditions. High (≥ 0.26), moderate (0.16 to 0.26), and low (<0.16) dominance.

Maps of model outputs show distinct changes in high- and low-dominance areas in some portions of the basin (Map set 8.2), although changes are not as evident as those in richness. Areas of high dominance expand with increasing development in South Lake Tahoe, Round Hill/Zephyr Cove, east of Stateline, along the east shore up to Spooner Lake, Incline Village, and even the far reaches of the Upper Truckee watershed. Changes in high-dominance areas are accompanied mainly by increases in moderate-dominance areas. Low-dominance areas are less obviously affected.

Richness of ground nesters

The final model for ground-nester richness retained 31 variables (shortened to 30 by dropping the variable with the smallest coefficient to meet the constraints of ArcGIS), with strong influences of elevation, 1000-m development, low-elevation conifer, aspen, riparian-meadow, high-elevation conifer, and UTM E (Appendix 8.1). The management scenarios had a slight effect on ground-nester richness because of their alteration of development, but a smaller effect than they did on total species richness.

Richness of cavity nesters

The final model for cavity-nester richness retained 32 variables (shortened to 30 by dropping the two with the smallest coefficients to meet the constraints of ArcGIS), with strong influences of canopy cover, brightness, distance to water, 300-m and 500-m development, NDVI, and 500-m shrubs (Appendix 8.1). The management scenarios had a strong effect on cavity-nester richness because of the scenarios' alteration of development, canopy cover, and NDVI.

Small Mammal Models

The GIS models for small mammal species richness and relative abundance retained 14 variables each (Appendix 8.1). They revealed that factors related to human development, vegetation, and habitat type had predictive power. However, the relative influence of these factors on species richness and relative abundance did vary. For species richness, development at the 1000m-scale had the strongest relationship with the number of species observed at a site. This relationship was quadratic in nature, with higher species richness realized at sites in the middle of the development continuum. We found a similar association between species richness and development at the 500m-scale, but this relationship was not as strong. Relative abundance was also positively influenced by development at these scales, but this relationship was linear. These results indicate that urbanization alone is not necessarily detrimental to small mammal species. In fact, moderate levels of development may be facilitating the coexistence of species, possibly due to land management practices aiming to reduce fire threat coincidentally improving habitat conditions for a variety of small mammals. However, it is important to note that species richness was slightly lower at sites with very low or very high development. The results of these predictive models indicate that a high degree of development across the landscape could ultimately have detrimental impacts on small mammal biodiversity.

In addition to predictive value of urban development, we found that the percent cover of shrubland (as defined by CWHR habitat types) was positively associated with small mammal species richness. This relationship was due to greater variability in the number of species observed at sites with lower shrub cover, which reduces the average number of species observed at these sites. Sites with greater than 7% shrub habitat within 500m consistently supported no fewer than 4 different small mammal species, which indicates that shrub cover is an important habitat component for some small mammal species.

The factor that exhibited the strongest relationship with small mammal relative abundance was the normalized difference of the vegetation index (NDVI). NDVI is a measure of vegetation amount and condition and is associated with vegetation canopy characteristics (e.g., biomass, leaf area index and percentage of vegetation cover). Of the sites included this analysis, NDVI ranged from 0.32-0.64, and abundance was highest at sites at the lower half of this range (NDVI = 0.32-0.50). Similarly, small mammal abundance and species richness were also negatively related to factors related to canopy cover and tree density (e.g., brightness, bare ground cover). Therefore, small mammals were found to be more speciose and abundant at sites with lower average vegetation cover, presence of shrubs, and some amount of bare ground. In Chapter 3, regression models identified the percent cover of bare ground at a site to be an important factor positively associated with small mammal abundance. Since the predictive models were limited to only those variables that could be obtained or modeled through GIS layers, the percent cover of bare ground was not included in these predictive models. Without information on site-specific habitat features, the GIS models indicates that NDVI and brightness may be useful surrogates for characterizing some of the local site conditions to which small mammal mammals are responding.

** maps to be developed

Carnivore Models

Model averaging produced a final GIS-model for marten consisting of 21 variables (Appendix 8.1). The probability of marten occurrence was negatively associated with development at multiple spatial scales (300, 500, and 1000m) and positively associated with brightness and the occurrence of meadow habitats within 1000m.

Predicted probabilities of occurrence across the landscape were placed into three categories based on the distribution of values, most of which were near 0 or 1: high (≥ 0.90), moderate (0.60 to 0.90), and low (< 0.60). The results of the landscape modeling scenarios for marten suggest only slight shifts in probability of occurrence in response to the extent and location of development (Fig. 8.4, Map set 8.3). This may reflect the spatial distribution of parcels that are eligible for development which is likely to be concentrated at lower elevations, closer to Lake Tahoe. This would tend to reduce the overlap of areas of marten occupancy with eligible parcels minimizing impacts of future development. It is likely that the probability of marten occurrence in the Lake Tahoe Basin is at greater risk from high elevation recreational and residential development rather than from the development of lower elevation private parcels or public urban lots.

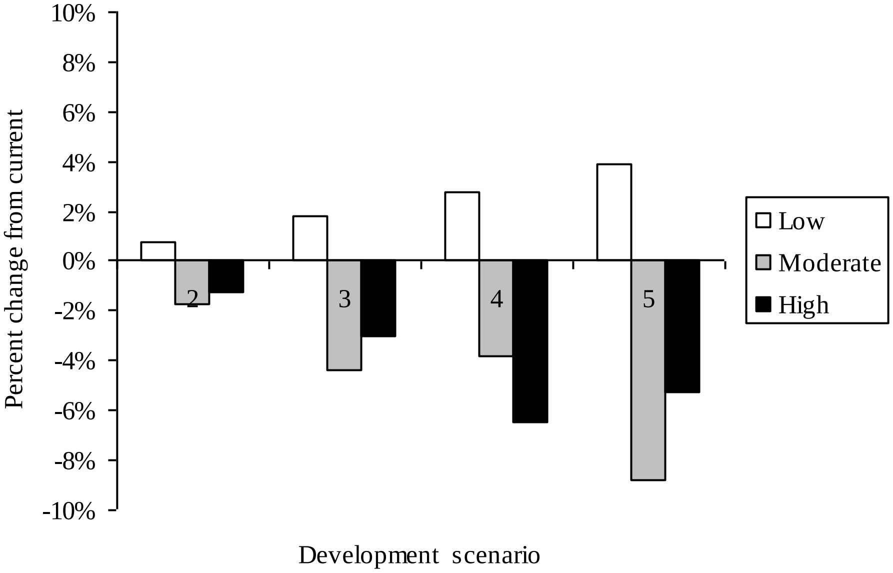


Figure 8.4. Change in proportion of the landscape in each of three occupancy probability classes for marten. High (≥ 0.90), moderate (0.60 to 0.90), and low (< 0.60) probability of occurrence.

Twenty-two variables were retained in the model averaging analysis for coyote (Appendix G). Coyote occurrence was negatively associated with amount of forest, NDVI, greenness, and development within 100 and 300m, and positively associated with amount of shrub types (at 300m and 1000m scales), amount of meadow types within 1 kilometer and development within 500 and 1000m.

Predicted probabilities of occurrence across the landscape were placed into three categories based on the distribution of values, most of which were near 0 or 1: high (≥ 0.90), moderate (0.60 to 0.90), and low (< 0.60). Under the development scenarios, the probability of coyote occurrence generally increased with increasing development although the change was slight (Fig. 8.5, Map set 8.4). Given the scale-dependent response of coyote to development and their association with open habitats (eg. shrubs and meadows), it is likely that coyotes could benefit from some level of development as long as some native habitats exist within 500 – 1000m.

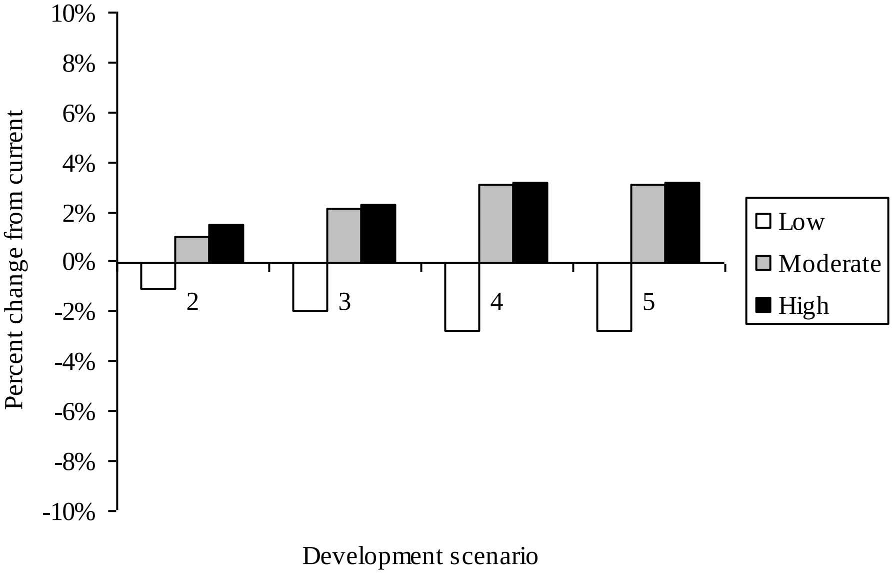


Figure 8.5. Change in proportion of the landscape in each of three occupancy probability classes for coyote: high (≥ 0.90), moderate (0.60 to 0.90), and low (< 0.60) probability of occurrence.

Ant Models

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Plant Models

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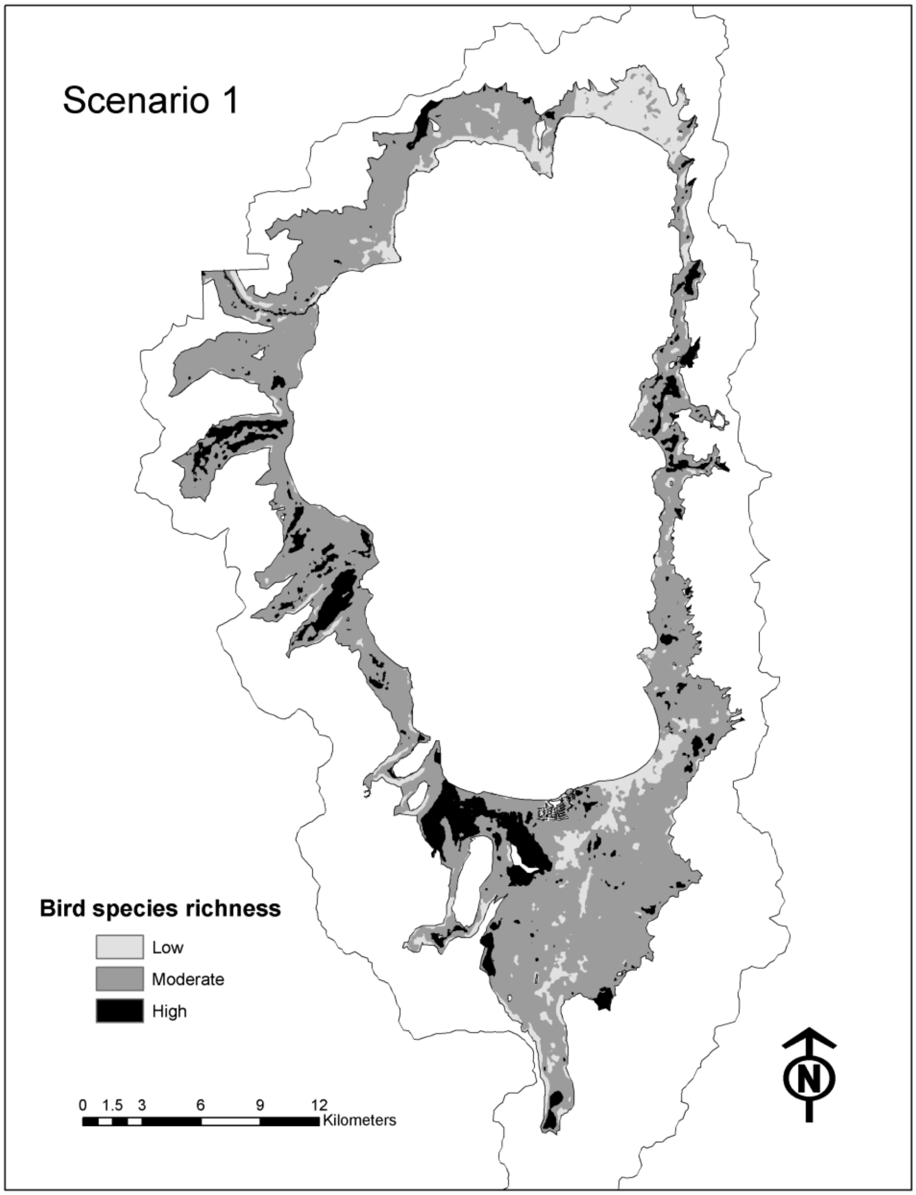
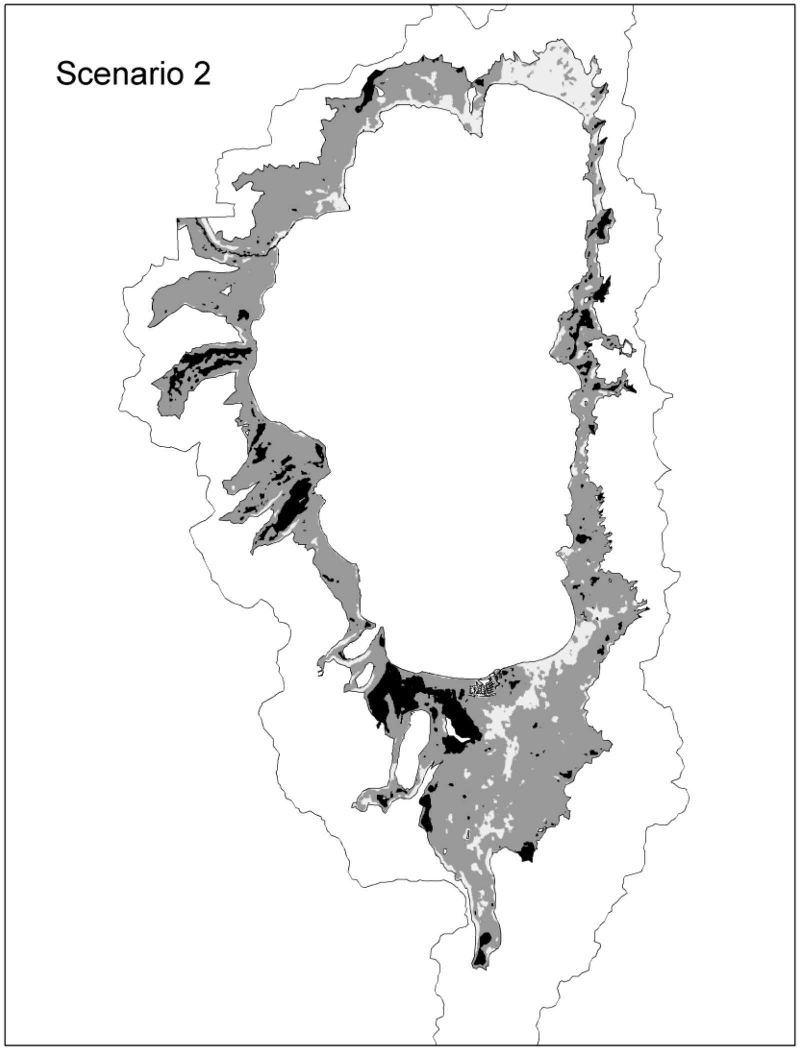


Map set 8.1. Five models of bird species richness given existing and potential future landscape conditions. Scenario 1 = existing conditions. Scenario 2 = 50% of private lands developed (50% coverage). Scenario 3 = 100% of private lands developed (50% coverage). Scenario 4 = Scenario 3 + all urban public parcels developed (10% coverage). Scenario 5 = Scenario 3 + urban Forest Service parcels developed (50% coverage).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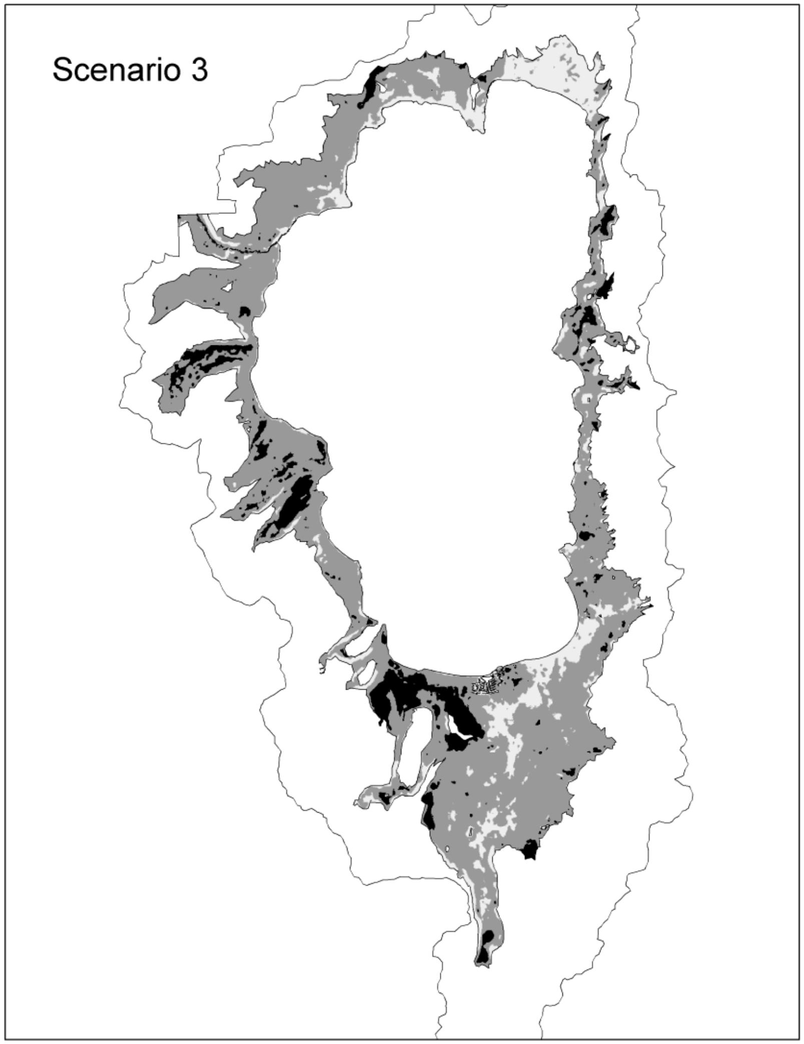
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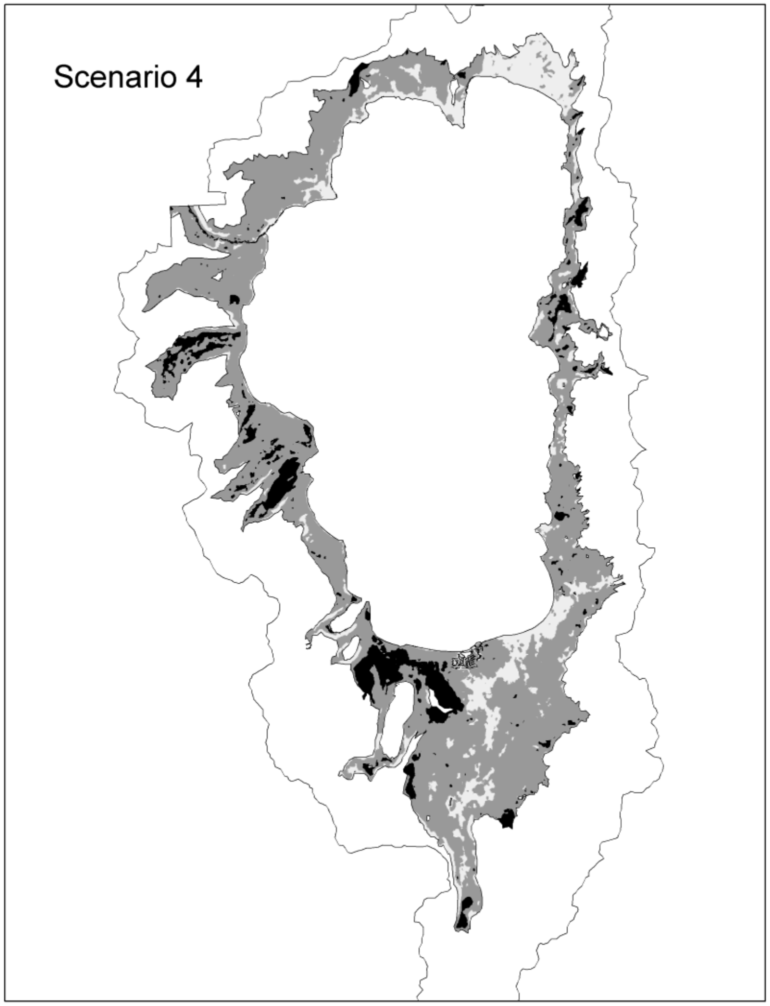
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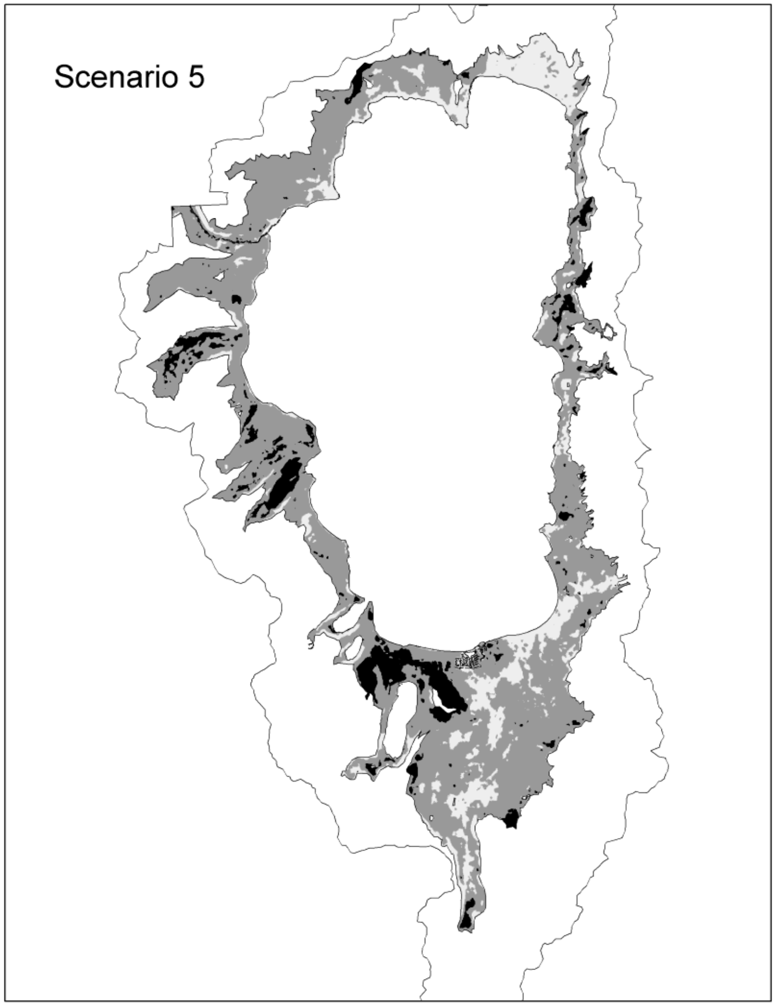
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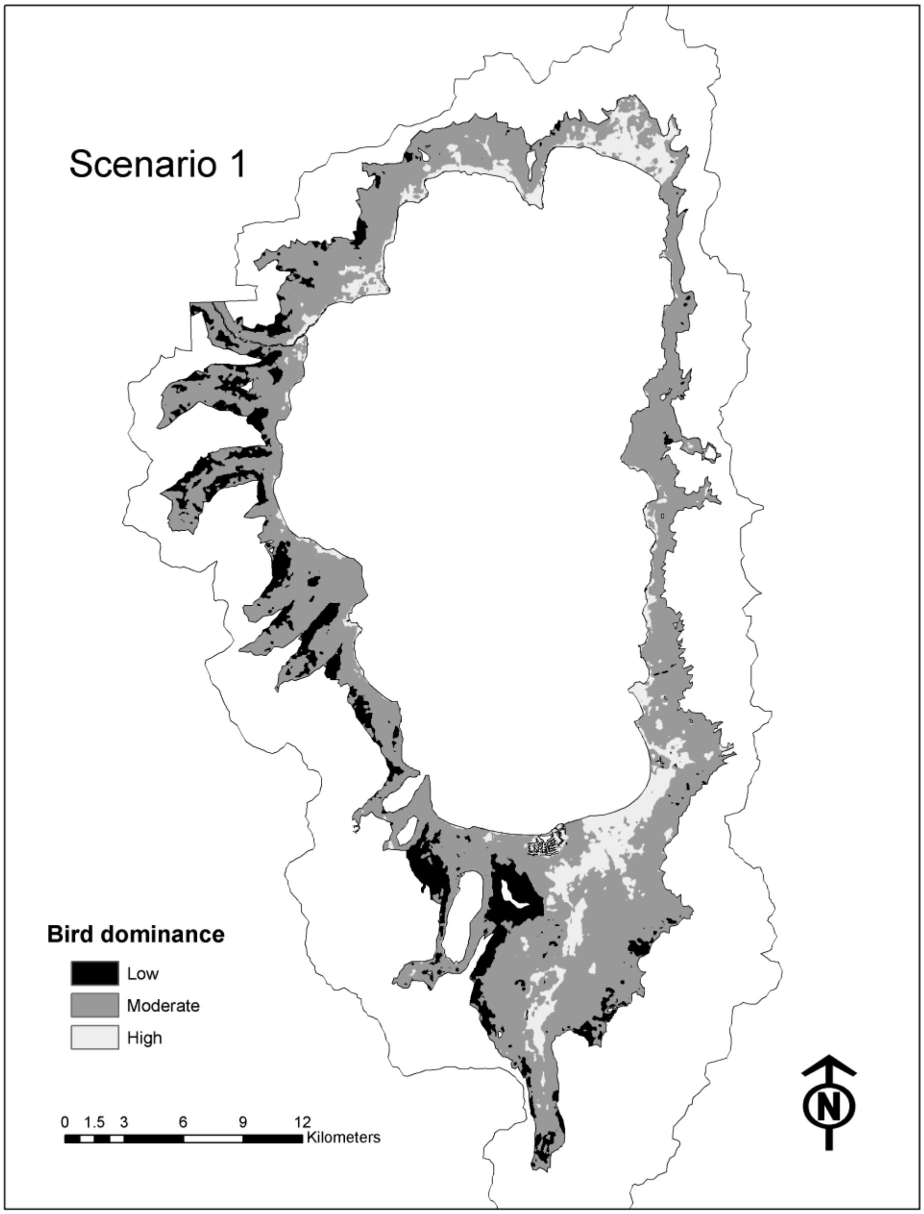
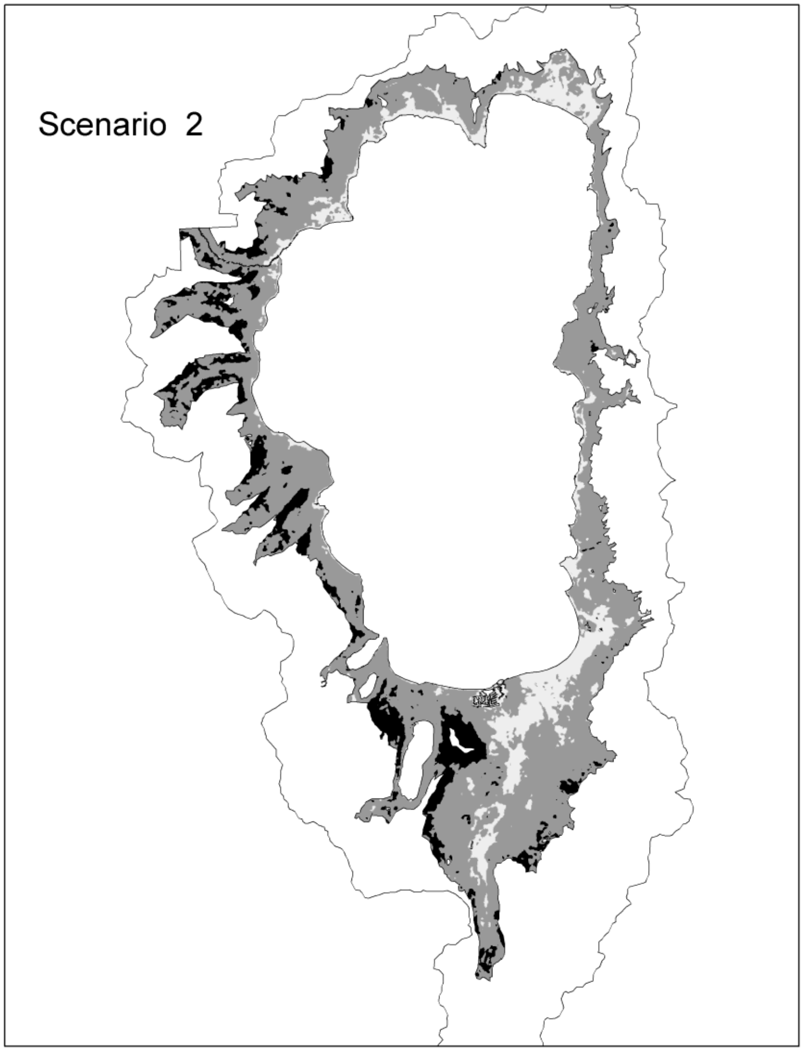


Map set 8.2. Five models of bird dominance given existing and potential future landscape conditions. Scenario 1 = existing conditions. Scenario 2 = 50% of private lands developed (50% coverage). Scenario 3 = 100% of private lands developed (50% coverage). Scenario 4 = Scenario 3 + all urban public parcels developed (10% coverage). Scenario 5 = Scenario 3 + urban Forest Service parcels developed (50% coverage).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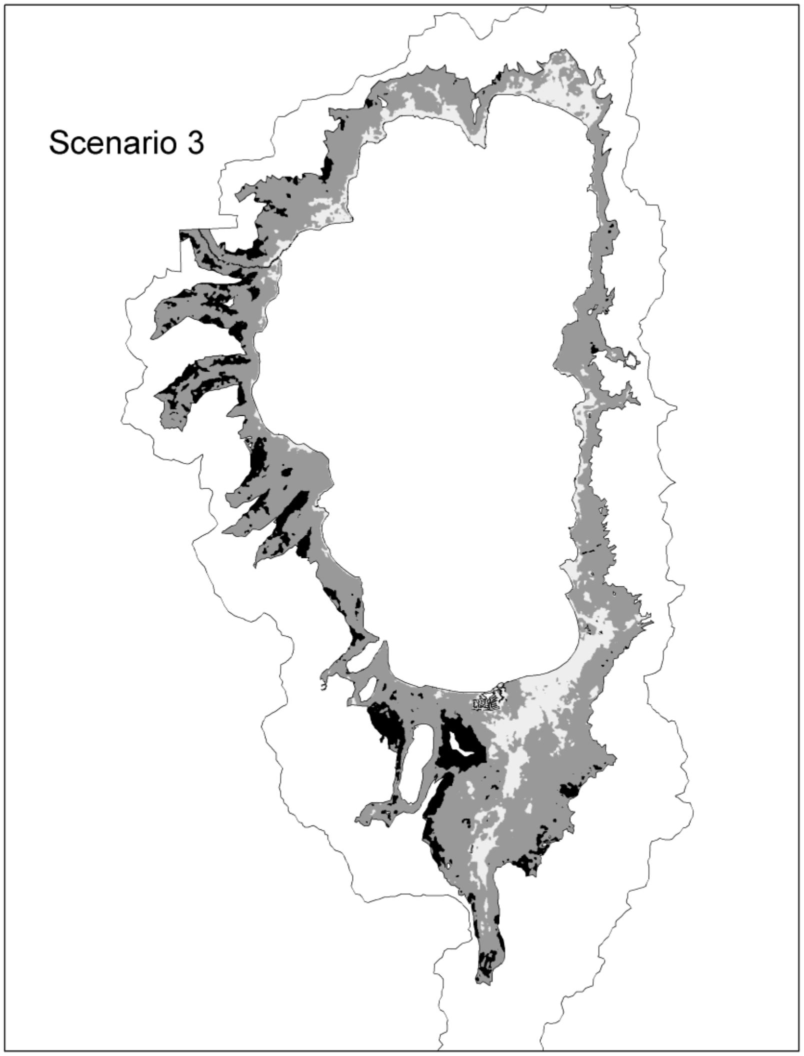
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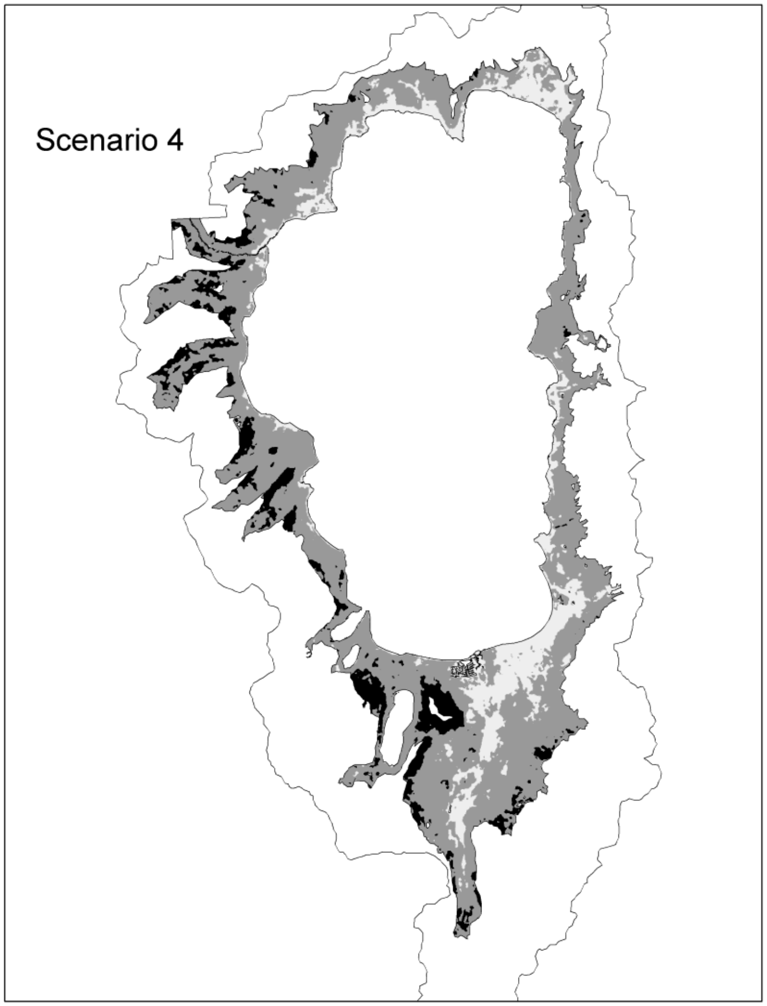
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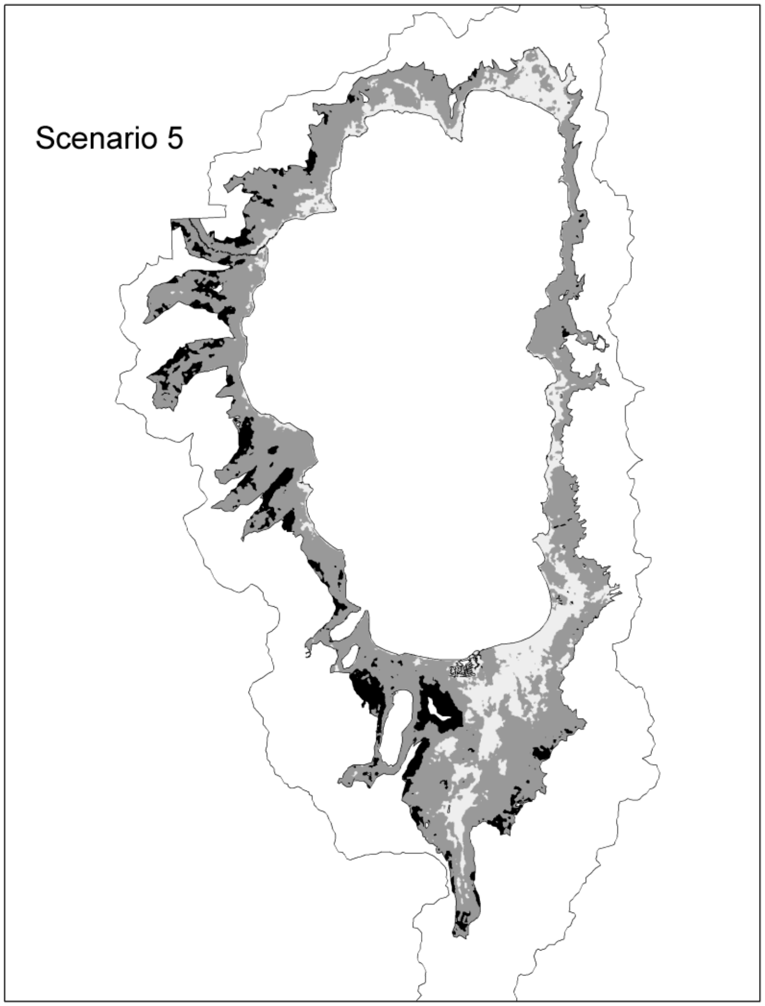
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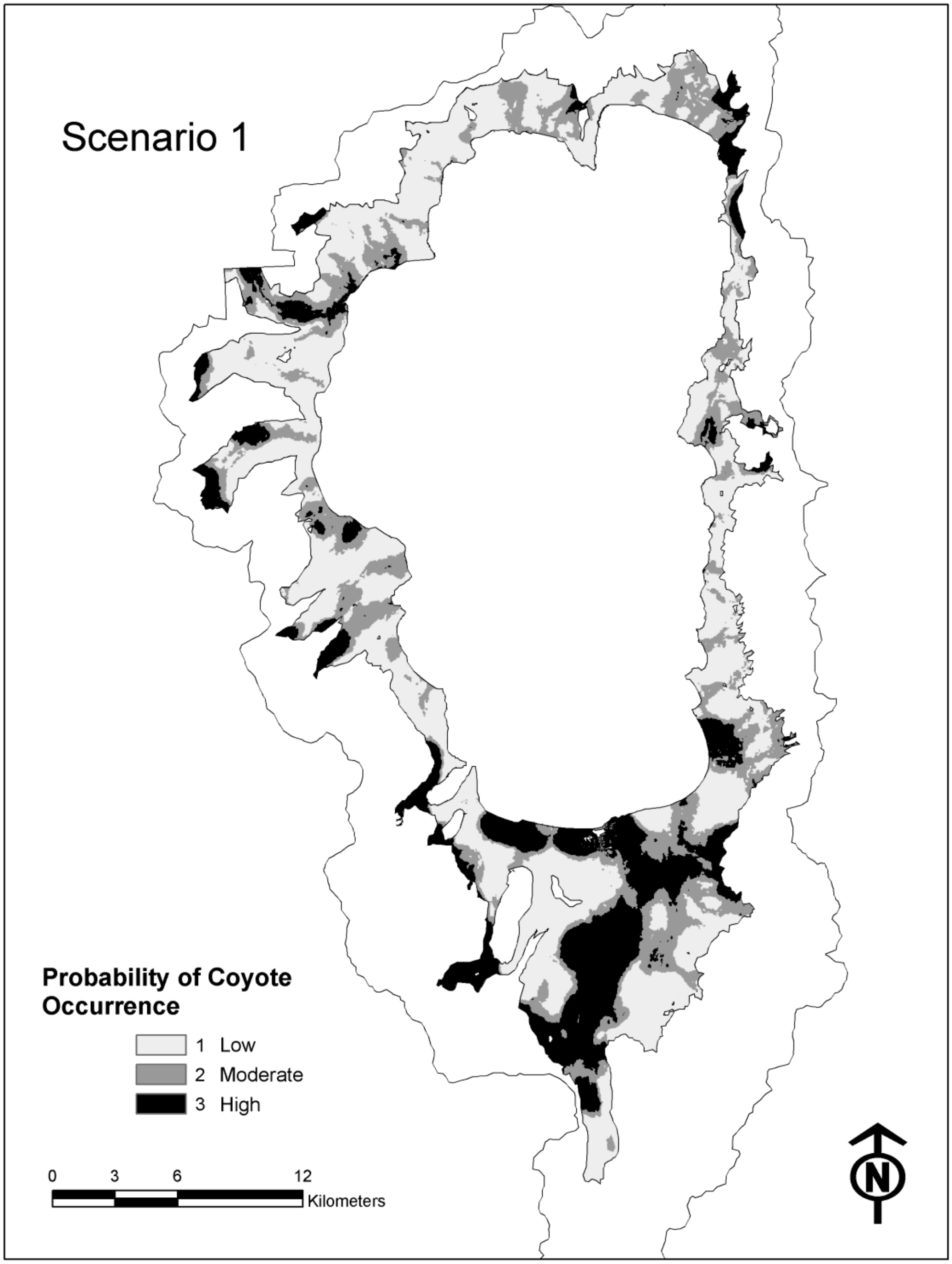
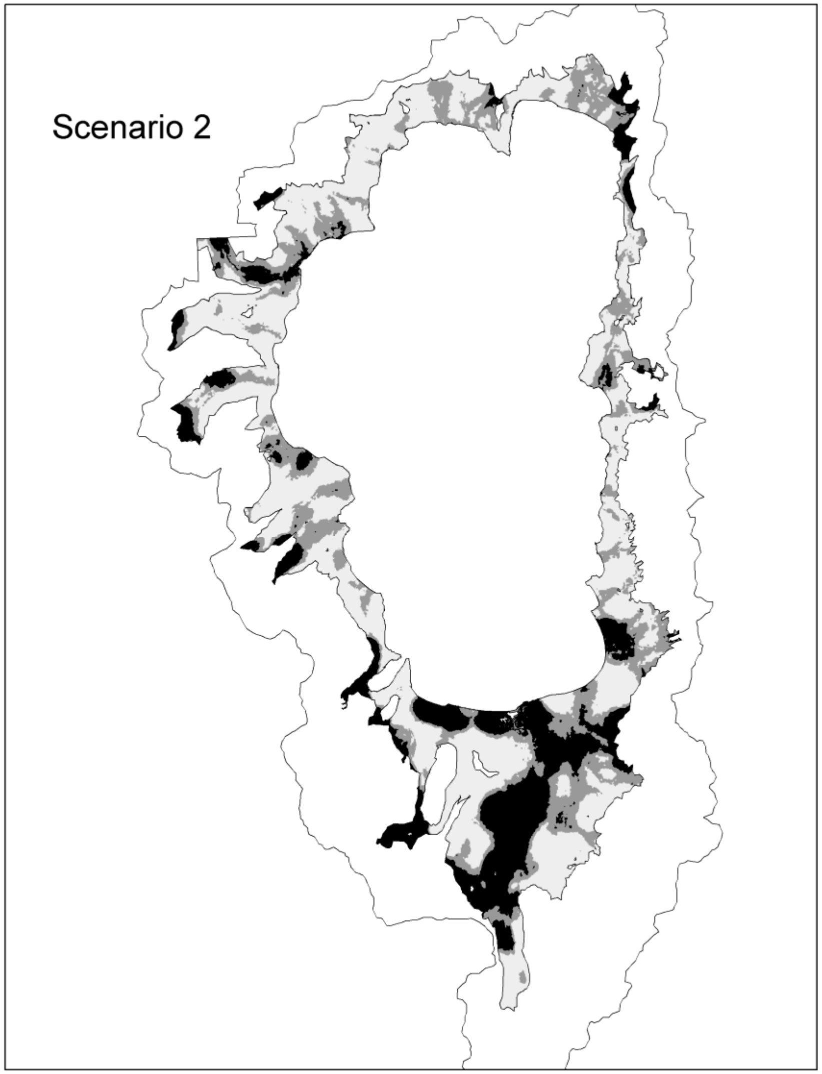


Map set 8.3. Five models of probability of occurrence of coyote given existing and potential future landscape conditions. Scenario 1 = existing conditions. Scenario 2 = 50% of private lands developed (50% coverage). Scenario 3 = 100% of private lands developed (50% coverage). Scenario 4 = Scenario 3 + all urban public parcels developed (10% coverage). Scenario 5 = Scenario 3 + urban Forest Service parcels developed (50% coverage).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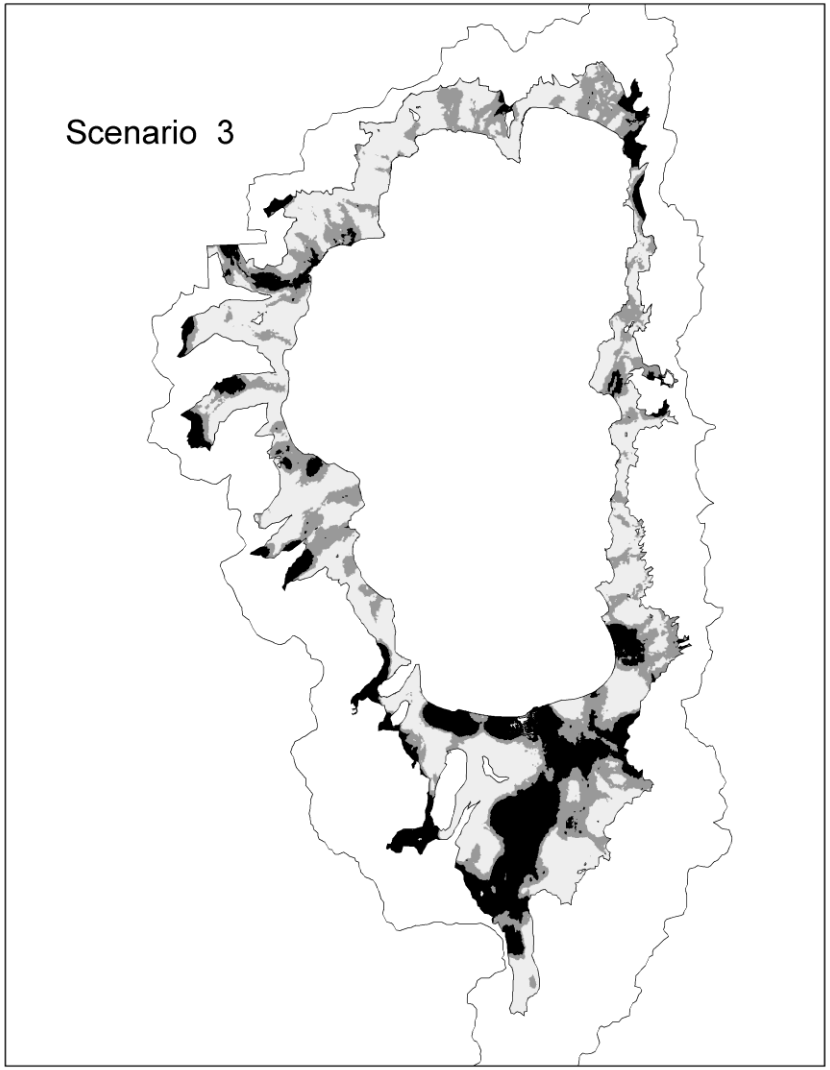
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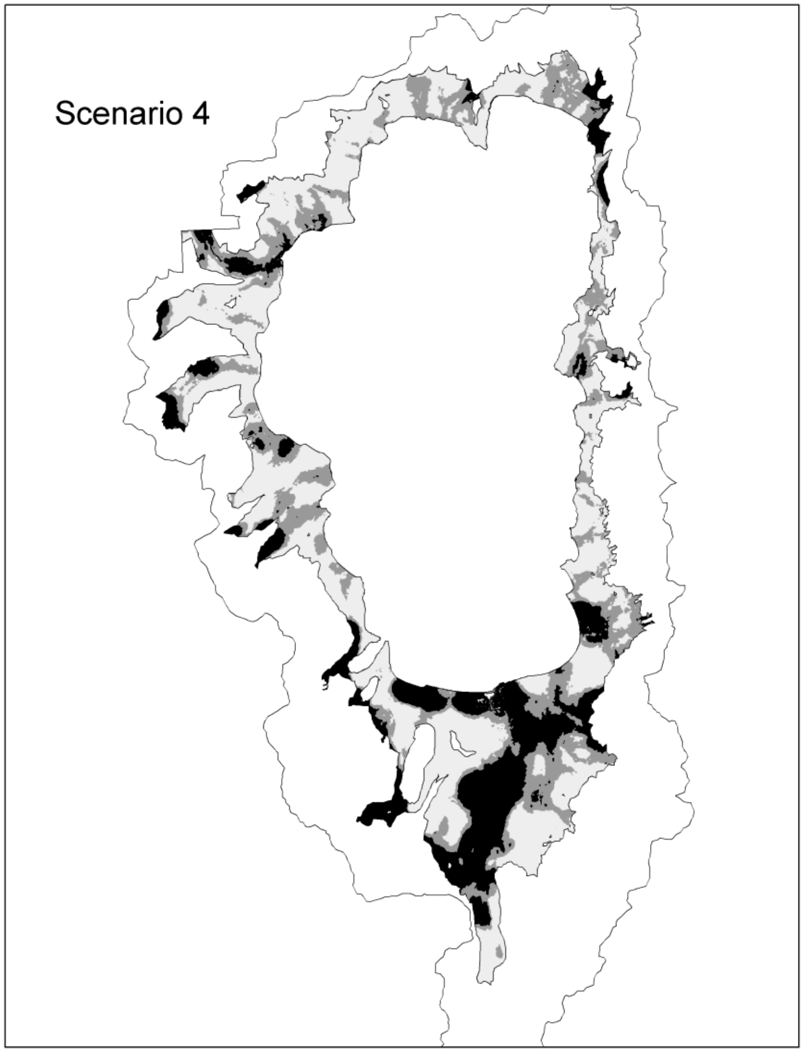
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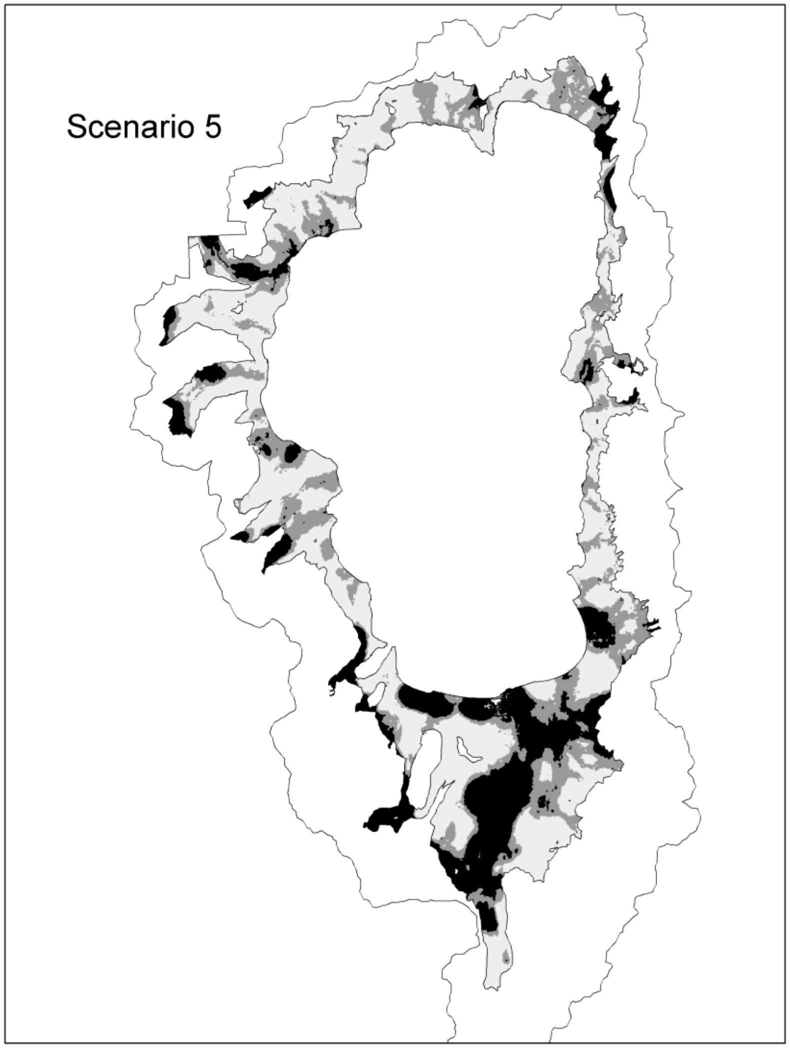
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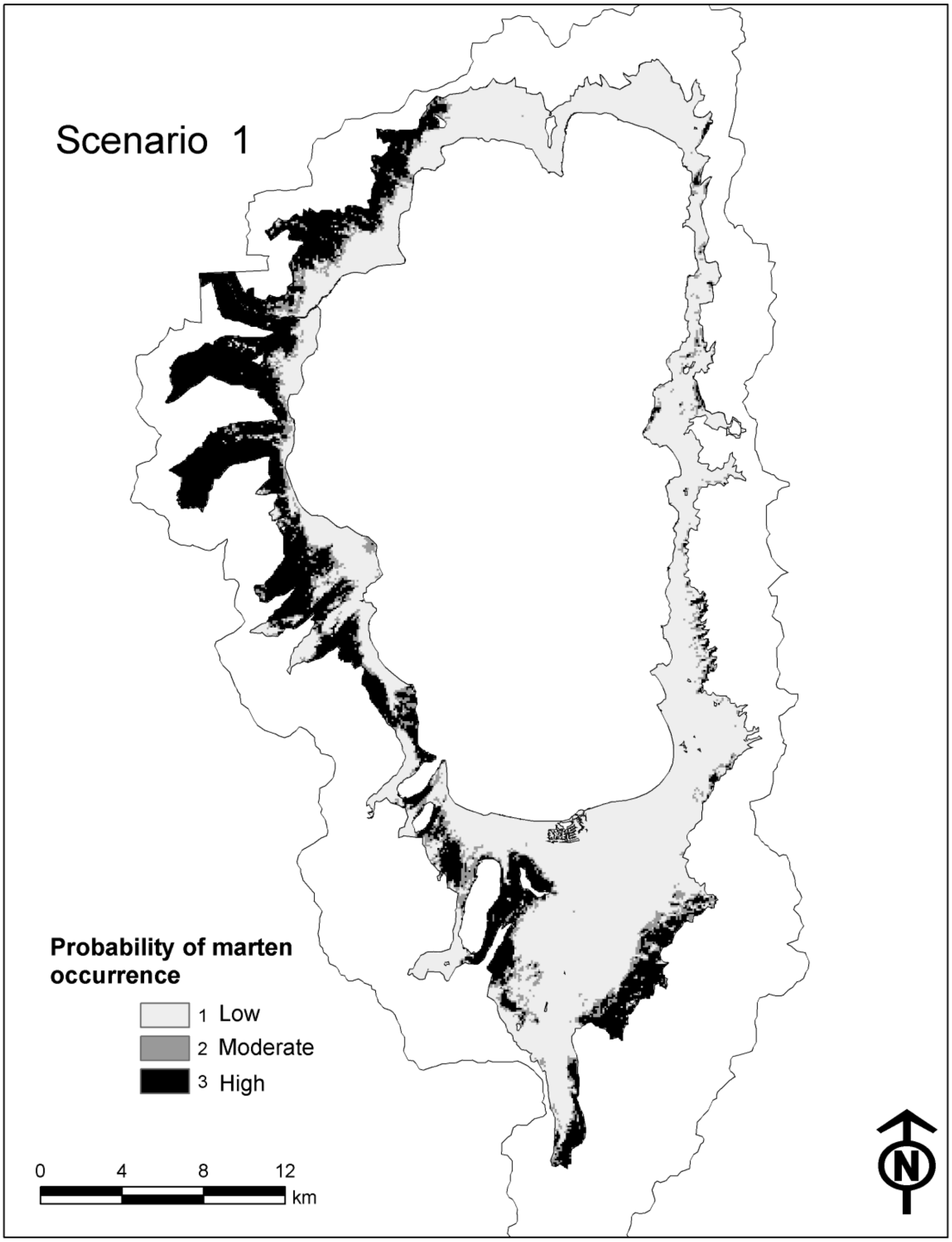
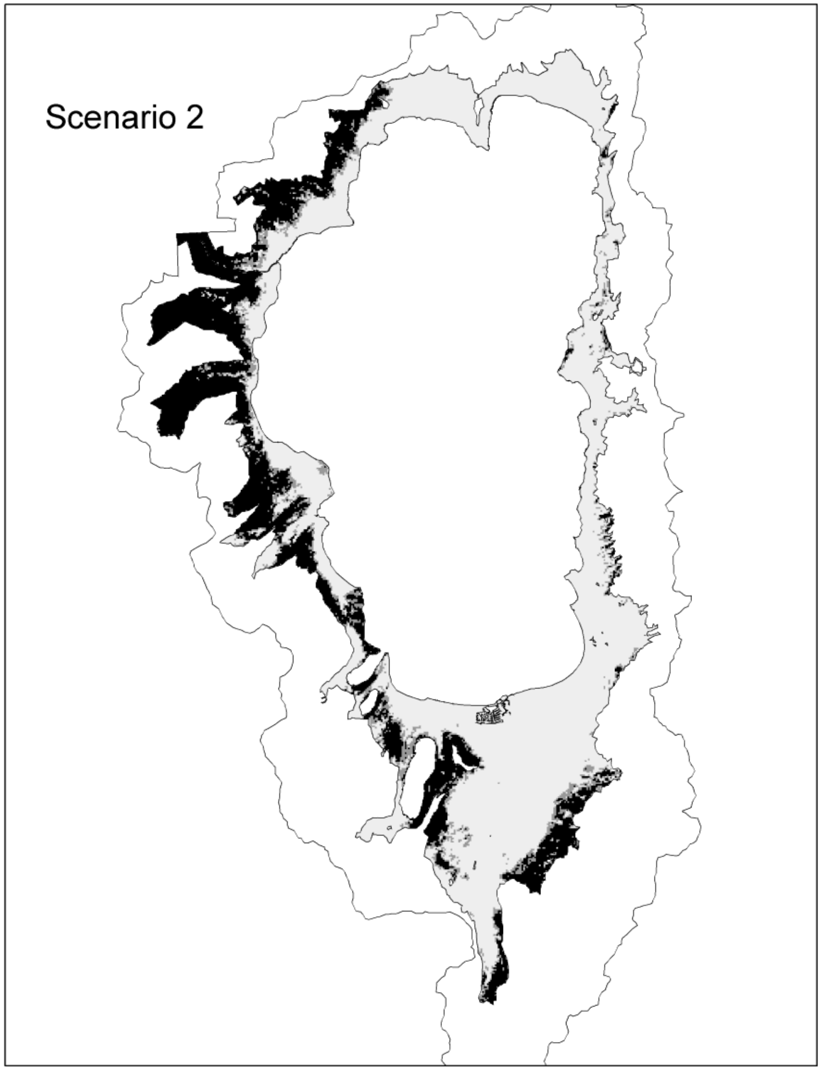


Map set 8.4. Five models of probability of occurrence of marten given existing and potential future landscape conditions. Scenario 1 = existing conditions. Scenario 2 = 50% of private lands developed (50% coverage). Scenario 3 = 100% of private lands developed (50% coverage). Scenario 4 = Scenario 3 + all urban public parcels developed (10% coverage). Scenario 5 = Scenario 3 + urban Forest Service parcels developed (50% coverage).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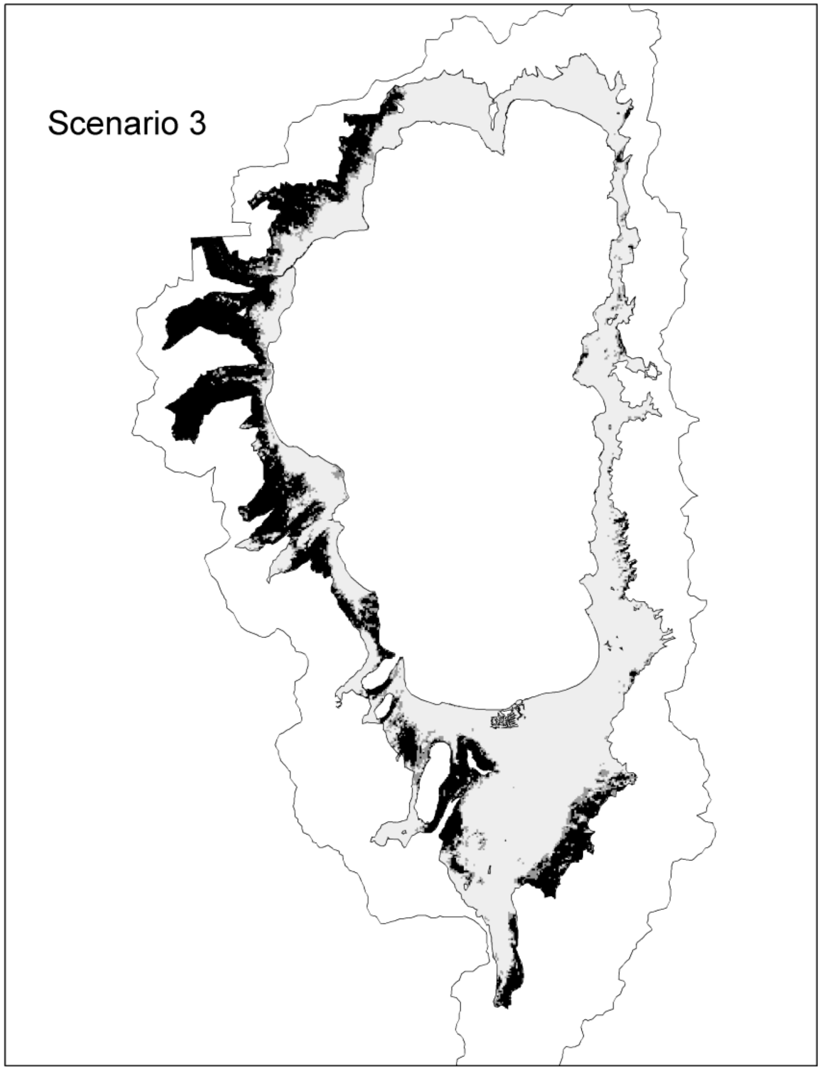
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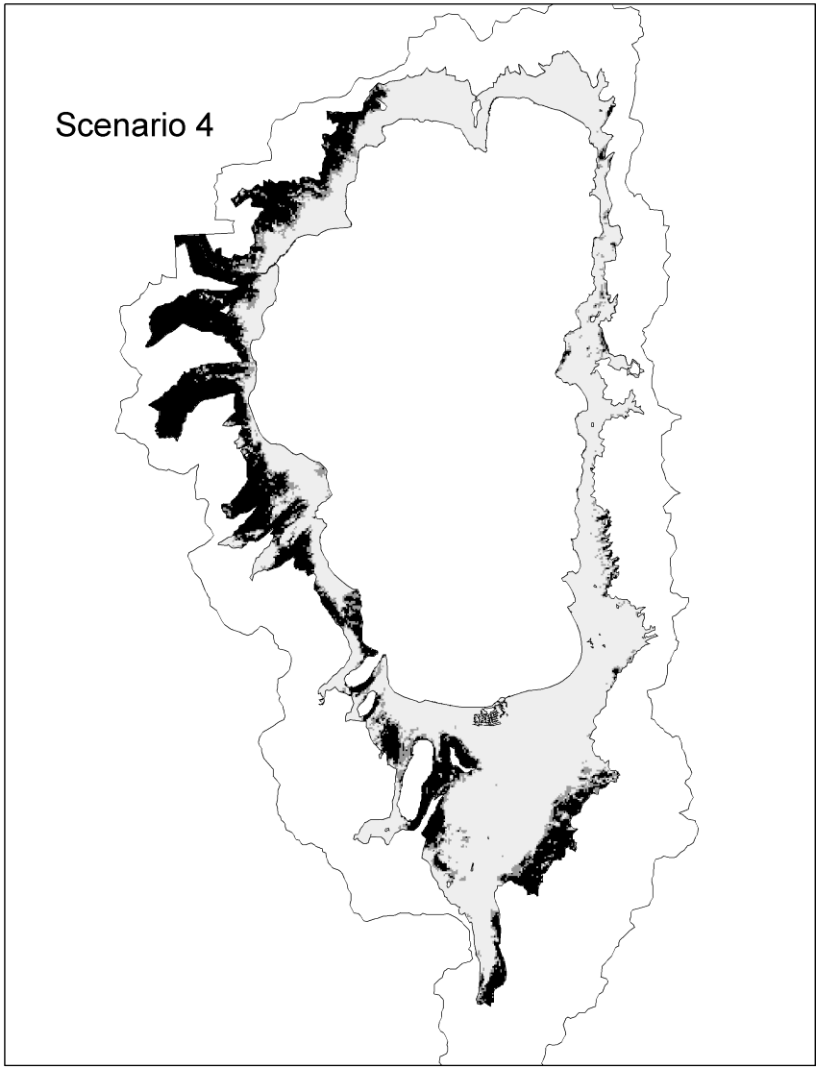
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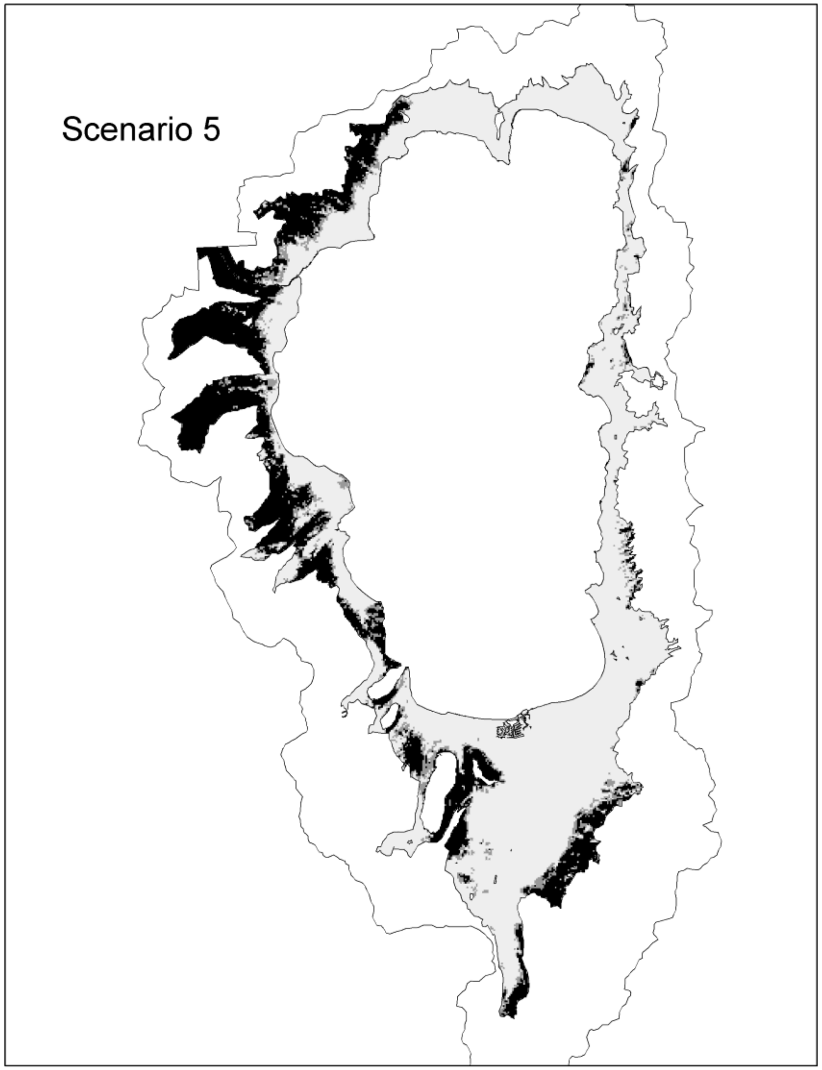
Scenario 5

Chapter 9:

Key Findings and Management Applications

This chapter summarizes the key findings for each taxonomic group and the landscape models from the associated preceding chapters. Further, the findings are interpreted in terms of the three primary management applications – development, assessment, and management. Development was interpreted in broad terms, including many types of development such as trails, roads, small-scale public service developments, housing developments, and commercial development. Assessment was interpreted as the ability to determine the relative degradation of biological diversity. We considered any biological metrics as potential indicators if they showed a strong and consistent relationship with development and/or human activity and were feasible to measure reliably. Management was interpreted as regulation of various types of human use, including recreation, domestic animal management, and vegetation treatments leading to changes in forest structure, tree size, tree density, understory cover, snags, or logs.

Human Use

Development

1. Development levels do not necessarily dictate human use levels; however, for the purposes of summarizing key findings, human uses are discussed under the heading of development as opposed to management.
   - Human use and number of vehicles were slightly greater in more developed areas, but these relationships were weak, indicating that development and human disturbance are not necessarily confounded.
   - Use was highest in June and July, with equivalently lower use levels in May, August and September.
   - Use was approximately 40% greater in afternoons (> 1 pm) compared to mornings (< 1 pm). This indicates that species most active in the afternoon or early evening would experience more disturbance than those active at other times of day.
   - Use was approximately 40% greater on weekends and holidays compared to weekdays. This indicates that use levels fluctuate, with periodic high levels of use.
   - The number of dogs was marginally greater in more developed areas. Nearly 75% of all dogs detected were unrestrained; however, dogs were more likely to be restrained in more developed areas.

Assessment

2. Facets of human use have various effects on biological diversity.
   - Some measures of biological diversity were affected by people, and others by dogs or vehicles.

    - All three of these measures are readily obtained, but people and dogs are most readily managed.
    - We suggest that use monitoring include measures of the type and intensity of direct use by people (e.g., walking, jogging, bicycling) and dogs on and off leash.
    - Direct or indirect measures of use can be effective in providing a relative measure of human use. Absolute measures of use are difficult to obtain with indirect sampling techniques.

Management

3. Unleashed dog use has the potential to have high impacts on wildlife.
    - The effects of dogs are discussed in association with individual taxonomic groups.
        - Given that unleashed dogs were more prevalent in less developed areas, it would be difficult to reduce dog disturbance through regulation.
        - Education can be an effective method to reduce the effects of human use.
        - It would be prudent to identify areas where controlling use (people or dogs) would have the greatest positive effect. For example, sites that have high biological diversity, unique species, unique habitat conditions, or key stepping stone remnant forests in the urbanizing landscape.

Birds

General

- Sixty-seven bird species were detected and analyzed. Species richness per site ranged from 5 to 28.
- A total of 671 nests of 29 species were located, and 566 nests were monitored for productivity.
- Strong relationships were observed between bird community and species metrics and urbanization metrics, as well as other environmental variables – they are discussed by management objective below and summarized in Appendix 9.1.

Development

1. Changes in species composition, species diversity and abundance of individual species with increasing development, and strong associations with the amount of forest in the landscape, suggest that urban lots and other remnant forests serve as valuable habitat for birds in the Lake Tahoe basin.
    - Bird species richness declined steadily with increasing development.

        - We did not find the peak in diversity at moderate development that some other studies have found.
    - Bird species composition changed substantially along the development gradient.
        - This change was driven by many different species, mainly ones more frequently occurring at either the low or high end of the gradient.
        - The most common species that were less frequently associated with development were Dusky Flycatcher, White-breasted Nuthatch, Hermit Thrush, Cassin's Vireo, Pileated Woodpecker, Hairy Woodpecker, Chipping Sparrow, Hermit Warbler, and Townsend's Solitaire (based on MRPP).
        - The most common species that were more frequently associated with development were Brewer's Blackbird, Band-tailed Pigeon, Barn Swallow, and Tree Swallow (based on MRPP).
    - Bird abundance was most closely associated with local and landscape vegetation, and secondarily human activity
        - Most bird species groups were positively associated with the amount of forested vegetation in proximity to the site (150-500 m), suggesting that local-scale fragmentation is a consideration in maintaining robust populations of bird species.
        - Abundance of individual species groups were associated with local vegetation features most relevant to their niche – invertivores responded to canopy cover, ground nesters responded to herb cover, cavity nesters responded to snag densities.
        - Cavity-nester abundance declined with declines in snag volume – results suggest that snag volumes > $10m^3$/ha were required to begin to support the full range of cavity-nester abundance observed across undeveloped sites.
        - Ground-nester abundance was negatively associated with human use and positively associated with aspen-riparian ecosystems, as well as conifer forests.
    - The abundance of over half the bird species analyzed was negatively or positively affected by development.

2. Productivity as a function of nest success was evaluated and species were either neutral or negatively affected by nearby development.
    - Development within the neighborhood around the nest (300 m) had limited effect on the daily survival rate of open-nester or cavity-nester species groups.
    - Development within close proximity to nests (50 m) had a negative effect on daily survival rate of open-nester and cavity-nester species groups, with open-nesters associated with shrub and ground locations faring worse than those located in the understory.
    - Nest success declined with development for three of 10 species examined in detail: Steller's Jay, Pygmy Nuthatch, and Dark-eyed Junco. Additionally, Dusky Flycatcher did not even nest in urban areas (development > 10%). While this might not seem like a large proportion, consider that these 10 species were among the most common in the basin

    - Nest success was high for cavity nesters and considerably lower for open nesters, whose success was lower with increased development. Among open nesters, shrub and ground nesters fared worse than tree nesters.
    - Western Wood-pewee abundance declined with increasing development, and its nests were lower to the ground in developed and high-use areas -- heights at which they were less successful. In other words, urbanization appears to reduce pewee nest success indirectly through nest height. This result highlights the Western Wood-pewee as a potential species of concern in the urbanizing Lake Tahoe basin.
    - Human structures were used for nesting by some species, mostly cavity nesters: Northern Flicker, Mountain Chickadee, Pygmy Nuthatch, White-breasted Nuthatch, White-headed Woodpecker, and Steller's Jay. The reduced density of snags in more developed areas may precipitate greater use of human structures. Thus, two of the impacts resulting from the lack of snags may be sites becoming population sinks for cavity nesters, and damage to human structures from cavity excavation.
3. Urban areas may serve as "ecological traps" by attracting species that experience lower nest success there. At present, there is scant evidence to suggest that native forests should be managed to discourage nesting by certain species. To demonstrate ecological traps more convincingly, behavioral studies that demonstrate a preference for urban areas would be necessary.
    - Two species—Pygmy Nuthatch and Steller's Jay—were more abundant in urban areas but less successful in nesting, suggesting that urban areas may serve as ecological traps for these two species.
    - Dark-eyed Junco, the only ground nester for which we had nest success data, both declined in abundance and in nest success in urban areas. It appears that more developed areas may be an ecological trap for ground nesters in general, given that their abundance was only slightly negatively associated with development, but their nest success was greatly reduced in more developed areas. Not only was nest success reduced, but we were unable to locate many ground nests of any species in urban areas.
    - Cavity nesters nested lower to the ground in high development than in low development, where they may be more susceptible to nest predation and disturbance from people. Lower nesting likely resulted from reduced availability of tall snags and increased use of human substrates.

Assessment

4. Several species and species groups were strongly associated with development and human activity and could potentially be used to demonstrate the condition and contribution of native forests in urban areas.
    - Potential indicators of compromised bird communities resulting from urban conditions include high abundance of Brewer's Blackbird, Brown-headed Cowbird, and Steller's Jay; high abundance of ground-foraging omnivores; and low overall species richness.

    - Potential indicators of undeveloped conditions include high abundance of Dusky Flycatcher, Hermit Thrush, Pileated Woodpecker, Western wood-pewee, ground nesters, and cavity nesters.
    - Surveys that characterize the entire bird community are recommended for assessment rather than targeted surveys for particular species.
5. Productivity data are not useful for assessing the value of particular urban forest remnants because they are aggregate measures over large numbers of nests, and they are expensive to collect.
6. Measures of habitat condition most relevant to the bird community include the following. At the site scale, the amount of development within 30 m, snag volume, tree density, shrub and herb cover, and canopy cover. At the landscape scale, amount of conifer vegetation, the amount of aspen and riparian vegetation, and development were most relevant.

Management

7. Disturbance from human use was of greater importance than habitat loss from development in many cases.
    - Human activity is a feature of development that can be controlled even in areas of high development, and therefore it is something that can be managed to achieve biodiversity objectives in key areas.
8. Ground-foraging omnivores were most associated with human use, which likely brings an increase in food resources for these birds.
    - Reducing bird feeding and controlling garbage could help reduce numbers of these species and create a more natural balance in the composition and abundance of bird species in the community.
9. Cavity nesters were most associated with local vegetation structure, especially snag volume. Cavity nesters also nested lower to the ground in higher development. This pattern likely resulted from lesser availability of tall snags, and greater use of human structures, in high development.
    - Retaining snags, and particularly large snags, within Tahoe's urban environments is vital to maintaining populations of cavity nesters there.
    - It is likely that the absence of snags encourages cavity nesters to bore holes in houses, causing significant property damage.
    - The apparent snag volume threshold of > 10 m^3/ha equates to an approximate minimum of 12 snags/ha (5 snags/ac) that are > 61 cm (24 in) diameter and > 3 m (10 ft) tall. In situations where snags are taller or larger, equivalencies can be calculated. Generally, taller and larger snags will receive proportionately less use per unit volume since birds use is confined to a smaller space (i.e., multiple species or individuals of the same species using the same snag). Example equivalents shown here reflect a 20% increase to account for fewer individual snags:
        - 7 snags/ha (3 snags/ac) > 61 cm (24 in) and > 6 m (20 ft) tall;
        - 6 snags/ha (2.5 snag/ac) > 91 cm (30 in) and > 6 m (10 ft) tall;
        - 4 snags/ha (1.6 snag/ac) > 91 cm (30 in) and > 6 m (20 ft) tall.

10. Invertivores were associated with local vegetation structure, specifically high snag volume, high canopy cover, and somewhat paradoxically, low tree density.
    - Managing these features of Tahoe's forests in conjunction could be a good first step in improving conditions for invertivorous birds.
11. The retention and restoration of aspen and riparian vegetation in urban forest parcels could help mitigate the potential impacts of development on ground-nesting and shrub-nesting birds.

Future Directions for Research

Our results have highlighted additional research that would be beneficial in expanding our knowledge of avian biodiversity in the face of urbanization in the basin. The importance of human disturbance in structuring the landbird community indicates a need for a deeper understanding of the mechanisms underlying its effects. Research into the behavioral responses to different types of activities, their duration, and their timing, would greatly benefit managers looking to control effects of such disturbance on birds. Additional investigations into bird behavior and responses to the novelty of urban environments would increase understanding of interspecies differences in responses to urbanization and yield information on appropriate mitigation strategies that might increase use of urban areas by some species. Management experiments that test the use of (and reproductive success in) artificial nesting structures for cavity nesters could help generate strategies for increasing use of urban areas by this key species group. Whether urbanization facilitates nest parasitism by Brown-headed Cowbirds is an important management question best addressed by nest monitoring of cowbird-sensitive species like vireos and warblers along the urban gradient, which were not target species in this study. Finally, use of human structures for nesting by birds in urban areas is an interesting ecological phenomenon and management concern -- under what conditions will birds nest in human structures? Does their willingness to nest in human structures affect their ability to survive in urban areas? How do nesting ecology and reproductive success differ in natural versus artificial nest substrates? How can damage to human structures be reduced or prevented?

Small Mammals

General

- Nineteen species of small mammals were sampled, ranging from 2 to 9 species per site.
- Squirrels and chipmunks were the dominant taxa (approximately 95% of all individuals) as opposed to mice, voles, woodrats, or shrews. Sciurids accounted for most of the species observed at a single site, with an average of 4 sciurid species per site. Of all the small mammals, long-eared chipmunks were the most evenly distributed across the basin, followed by California ground squirrels, deer mice and Douglas squirrels.

- By far the rarest species observed in the basin at forested sites below 7000ft elevation were lodgepole chipmunks, western jumping mice, bushy-tailed woodrats, and pinon mice.
- Relationships between primary measures of the small mammal community and environmental conditions, including human development and activity, are depicted graphically in Appendix 9.1 and discussed in detail below.

Development

1. We found limited impact of development on small mammal species richness or abundance; however, patterns of community composition did vary significantly with development.
    - The range of values observed in species richness decreased with development: the range of richness values spanned 2 to 10 species at sites with < 40% development, and reduced to ranging from 4 to 7 at sites with > 40% development.
        - This indicates that sensitive species drop out and species benefiting from development occur more regularly.
        - Species occurring less frequently with development were shadow chipmunk, deer mouse, long-eared chipmunk, and northern flying squirrel.
        - Species occurring more frequently with development were voles, Douglas squirrel, and to a lesser degree golden-mantled ground squirrel
    - Species richness was positively, linearly associated with development at 1000 m in the full regression models , however survivorship declined with development at 1000 and/or 300 m for most species.
        - These results indicate that higher levels of development in the larger landscape may result in species packing in the remaining undeveloped native forests.
        - Lower survival rates in forests with greater surrounding development suggest that at higher levels of landscape development native forests are likely to become population sinks, which means the persistence of species at these sites is dependent upon immigration from other sites.
6. Human disturbance had a positive effect on small mammal species richness.
    - Frequency of use by people was found to have a slight positive association with species richness. This is likely to the more frequent occurrence of synanthropic species, such as California ground squirrel and gray squirrel, that can benefit from lower predation and greater food resources that commonly correspond with increased human (and dog) use. In this study we found that carnivores either had an aversion to developed areas, or they changed their behavior patterns to be more nocturnal in developed areas.

    7. There was no patterned relationship between total relative abundance and development, but there was a negative relationship with human use.
        - Since the species detected in the highest numbers at all sites were ground squirrels and chipmunks that are both primarily terrestrial and diurnal, this pattern is likely a reflection of a direct interaction between human use and activities of these species.
    8. The frequency of dominance of many individual species shifted with development
        - Yellow pine chipmunk was more frequently numerically dominant as development increased, while long-eared chipmunk was less frequently dominant.
        - A similar, but less pronounced pattern was observed with California ground squirrel being more frequently dominant and shadow chipmunk being less frequently dominant.
    9. The relative abundance of arboreal squirrels (composed primarily of Douglas squirrels) was the only functional group associated with human stressors: it was positively related to development at the 1000m-scale and to the presence of domestic dogs (see above discussion of these factors).
    10. Three species were consistently more frequently occurring at sites with higher surrounding development: Douglas squirrel, yellow pine chipmunk, and voles.
    11. Long-eared chipmunk, shadow chipmunk, northern flying squirrel, and deer mouse were consistently less frequently occurring with higher surrounding development.
2. For all species analyzed, survival rates decreased and emigration rates increased as development intensity increased.
    - Species whose vital rates were most negatively affected by development were shadow chipmunk, lodgepole chipmunk, Douglas squirrel, California ground squirrel, and golden-mantled ground squirrel.
    - The combination of high frequency of occurrence, higher abundance, and lower vital rates for the Douglas squirrel and California ground squirrel at sites with higher development suggests that higher development sites may function as ecological traps for these species. Thus, these two species may be at some risk of population decline, perhaps quickly, if development exceeds some threshold of extent for this species in the basin.
    - Species whose vital rates were not greatly affected by development or human disturbance were long-eared chipmunk and yellow pine chipmunk. Yellow pine chipmunk had low estimated survival rates (< 0.15 under any circumstance), so or all our sample sites were poor quality habitat for this species.
    - As development pressure and disturbance increase, habitat conditions may decline to a point where populations of the small mammal species vulnerable to development effects may be reduced or eliminated in remnant forest vegetation.

Assessment

3. We found that forested sites in urban areas generally exhibit similar small mammal species diversity values (richness and abundance) comparable to the undeveloped areas, so species richness and total abundance are not strong indicators of development and human use.
4. The occurrence and abundance of a number of individual species would be good candidate indicators, including long-eared chipmunk, shadow chipmunk, and .
    - Species whose frequency of occurrence was negatively affected by development were long-eared chipmunk and shadow chipmunk. The shadow chipmunk is a particularly strong candidate because its vital rates were also affected; however, we do no suggest measuring vital rates given the high expense and complexity of obtaining these measurements.
    - Species whose dominance abundance and vital rates were negatively affected by development were lodgepole chipmunk, and golden-mantled ground squirrel.
    - Yellow pine chipmunk abundance is a consistent and reliable response to development, at least within undeveloped forests. If the landscape continues to be developed, yellow pine chipmunk populations may also begin to decline.
    - Abundance of Douglas squirrel appears to be greatly affected by development, but it is not likely to continue to increase with development if it progressed in the basin. It is more likely that its population would start to decline at higher levels of development at various scales, so it would not be a good indicator for assessing conditions. However, it is probably an important species for management to monitor (see management section).

Management

5. One of the important habitat features positively related to small mammal species richness and relative abundance was the percent cover of bare ground at a site.
    - Disturbance that creates bare ground at a site can facilitate early successional vegetation communities and increase variation in microhabitat conditions, and natural variability in forest conditions across the landscape has produced a suite of forest-dwelling species are uniquely adapted to exploit these types of conditions.
    - Fuels management activities are the most extensive activities occurring in native forests in the basin. The removal of some overstory vegetation is likely to benefit most small mammal species, however wide spacing of overstory trees can impact the ability of arboreal species to move through the forest, potentially increasing their risk of injury and predation. Also, post-harvest treatments such as chipping and mastication have the potential to eliminate bare ground across large areas of the forest floor, which is likely to have a detrimental effect on small mammal community

    - richness and abundance, including the abundance of many individual species.

6. Dominant vegetation communities influenced both species richness and total relative abundance.
    - Heterogeneity of vegetation types surrounding sites was positively associated with overall species richness and abundance.
    - Arboreal squirrel (primarily Douglas squirrel) relative abundance was positively related habitat heterogeneity around a site (within a 100m radius).
    - Terrestrial granivore (ground squirrel and chipmunk) relative abundance was influenced mostly by ground-level habitat components. In particular, the percent cover of bare ground and herbaceous vegetation were identified as the most important factors related to abundance in these species.
    - Herbivorous voles responded positively to development at the 300m-scale where suitable habitat conditions exist, and vole abundance was greatest at sites with >50% development. Since there were more perennial herbs and grasses, native and exotic, in urban areas, voles were likely responding positively to these specific vegetation components as opposed to development.
    - Shrew relative abundance was positively associated with the amount of montane riparian and conifer (RFR, SCN, SMC, WFR). The amount of Sierran mixed conifer and white fir habitat was positively related to abundance at both the site and the surrounding area.
7. Our results also indicate that habitat management can accomplish much to retain the diversity of small mammals and maintain robust populations.
    - Overall habitat heterogeneity at the site and landscape scales is important for small mammal species. A greater availability of different habitat types may facilitate the coexistence of a greater number of individuals as well as individual species. Therefore, managing for a diversity of vegetation types at both the local and landscape level should be a part of management objectives aimed at maintaining small mammal species diversity.
    - Maintaining native forest vegetation within the urban matrix will likely be important for facilitating greater survival rates and successful small mammal dispersal and movement among forest habitat patches, thus sustaining populations.
    - Maintaining or creating some bare ground in undeveloped forests will promote higher species richness without appearing to degrade habitat for any small mammal species. Within sites surrounded by high development, bare ground is frequently created through various human uses; it is in less developed sites that it may be less prevalent.
8. This research has identified at least one group of habitat specialists, shrews.
    - Shrew abundance was positively associated with montane riparian habitat and conifer habitat, and the percent cover of Sierran mixed conifer and white fir were by far the most important specific habitat types at local and landscape scales.

    - Management of riparian and conifer forest habitats across the urbanizing landscape will likely be very important in maintaining shrew populations in the lower montane zone.

9. Species that maybe sensitive to development on one or multiple ways but do not make good indicators, or which are simply vulnerable to habitat alteration because they are habitat specialists, are important to consider as “fine-filter” focal species to monitor as habitat conditions change over the landscape and over time in the basin. The species with these characteristics that were identified in this study include shrews, yellow pine chipmunk, and Douglas squirrel.

Future Directions for Research

The current research has been successful in identifying important factors and the nature of their influence on small mammal communities and populations within the Lake Tahoe basin. However, there are several areas of inquiry that should be considered in order to complete our understanding of how small mammals are responding to anthropogenic stressors. Improving our knowledge base will strengthen our ability to make predictions about the ramifications of increasing human pressures. Some additional research needs evident from the results of our research include: sampling at elevations above 7000ft, sampling and comparing different habitat types, characterization of long-term population trends, and characterization of population connectivity and movement patterns within the basin.

For our research, small mammal sampling occurred over a 3-year period during which considerable variation in population size was noted. While we have begun to understand how small mammals are responding to development, there is still considerable uncertainty. In particular, while we found that relative abundance did not appear to be negatively impacted by development, we did find compelling evidence that key population processes of survival and emigration are being negatively affected. What are the implications of these results on population persistence? It is important to monitor theses populations over time to assess long-term trends and trajectories in terms of small mammal population viability.

Additional sampling outside the scope of this project is also warranted. The sampling frame for this research was limited to forested habitat below 7000ft elevation. This was an excellent starting point for assessing the role of urbanization on small mammals, but we need to understand more about communities and populations throughout the basin. For example, we found that lodgepole chipmunks were patchily distributed and rare among the sites we sampled. However, this species is the dominant chipmunk south of the basin in Yosemite Valley (J. Patton *pers. com*.). Are lodgepole chipmunks rare in the Lake Tahoe basin, or did we sample below the lower elevational extent for this species in this region? Sampling populations at all elevations and orientations would significantly improve our knowledge base in terms of Tahoe basin small mammal species’ distributions and habitat affiliations. In addition, by only sampling forested sites, we missed sampling species associated with other habitat types, such as riparian areas and meadows. Notably, we caught no Belding’s ground squirrels (*Spermophilus beldingi*) and very few montane voles (*Microtus montanus*) in our sampling; however, these species are very likely to be captured in meadow habitats. It is important to understand the status of all basin species and how they are responding to human activity because responses can (and likely will) vary by species.

Another area for additional research is related to population connectivity and how urbanization impacts population structure. At the landscape scale, population connectivity affects a species' ability to respond to environmental change (Pease *et al* 1989). Connectivity is impacted by anthropogenic habitat modification that alters the degree of habitat fragmentation as well as the intervening matrix among suitable habitat patches (Lawlor 2003). Reduced gene flow can have long-term genetic and evolutionary consequences by increasing the influence of genetic drift and reducing genetic variation (Gilpin 1991; Lande 1994; Mills & Smouse 1994; Frankham 1995). While most forest-associated species in the Lake Tahoe basin do not appear to have reached a distribution threshold with respect to urban development, maintaining landscape linkages may be crucial for preventing the loss of species. Natural habitats in the basin are currently maintaining representative samples of species and habitats; however, they may not be sufficient to maintain ecologically functional landscapes. If population processes are being negatively impacted by development, as we found here, then remnant habitat patches may not be able to sustain populations in the long-term. Furthermore, if the matrix surrounding habitat patches becomes increasingly inhospitable to a level that it presents a dispersal barrier, then populations can become effectively isolated and species may be lost. Therefore, maintaining stable population dynamics in addition to interconnected populations of forest-associated species will be important in preserving basin biodiversity and will set the course for the forest community that will be realized in the future.

Genetic techniques could be used to determine connectivity and genetic distinctiveness among sites around the basin. Population genetic data could be used to assess hierarchical population structure and explore historical and contemporary gene flow among populations. Combining demographic information from mark-recapture data with genetic survey data would permit inferences about the impact of human development on connectivity of Tahoe basin species at multiple spatial and temporal scales. Furthermore, additional knowledge about population connectivity can also influence management strategies, because populations that are sufficiently differentiated may be managed as distinct units in order to maintain population persistence.

Large Mammals

General

- Eighty-six sample sites along the development gradient were surveyed using track plates and remote cameras: 75 of them had full arrays (4 trackplates, 2 cameras, and 16 pellet plots), and 11 had reduced arrays at the center only (1 trackplate, 1 camera, 4 pellet plots).
  - Composition, richness, and occurrence results were based on reduced arrays from all 86 sites.
  - Eight native carnivores were detected, as well as the domestic dog and cat. Carnivore species richness ranged from 1 – 6 species per sample unit.

    - Leporids (rabbits and hares) and black-tailed deer were also detected via pellet group plots.
- Relationships between primary measures of the large mammal community and environmental conditions, including human development and activity, are depicted graphically in Appendix 9.1 and discussed in detail below.

Development

1. Carnivore species richness was not as sensitive to increases in development as was community composition. Changes in species composition and the association of both carnivore and herbivore species richness with local forest conditions suggests that undeveloped parcels within developed areas may be important to the occurrence of these species.
    - Carnivore species composition differed along the development gradient.
        - Composition at sites at the lower end of the development gradient differed from sites with moderate or high development levels, indicating that the primary changes occurring in response to development occur at low levels of development (< 30 %).
        - Occurrence of the rare marten was the greatest contributor to differences in composition along the development gradient (based on MRPP), whereas occurrence of the broadly-distributed black bear tended to homogenize composition along the gradient
    - Carnivore species richness did not vary significantly with increased development.
        - Carnivore species richness was best described by microhabitat structure, abiotic conditions and local habitat composition. Volume of coarse woody debris, large trees and proportion of forested area within 300 m were all positively associated with carnivore richness and suggest the importance of local vegetation characteristics for maintaining carnivores in developing landscapes.
    - Herbivore species richness was most closely associated with local and landscape vegetation composition
        - Rabbits and hares (leporids) were more strongly associated with local and landscape level vegetation composition and structure than with human activity or development.
        - Deer, in contrast, were strongly associated with vegetation characteristics (e.g., shrubs and coarse woody debris), with development at local and landscape scales, and with human activity.
        - Both leporids and deer were negatively affected by the presence of dogs and tended to be negatively affected by the presence of vehicles. Both groups displayed a scale dependent response to development showing negative associations with development at the finest scales (e.g., within 100m) and positive associations at coarser scales (e.g., 300m, 500m or 1000m) suggesting the importance of remnant native habitats within developed areas.

2. Species varied in their associations with vegetative characteristics, development and human use.
    - Species predicted to either tolerate or benefit from association with anthropogenic resources (e.g., domestic dog and cat, coyote, and raccoon) were more strongly associated with anthropogenic variables than with vegetation structure, composition or abiotic influences.
3. In the GIS-based model averaging analysis, coyotes were positively associated with open habitats (eg. shrubs and meadows) and development within 500 or 1000m but were negatively associated with development within 300m or less.
    - Coyotes may be best able to exploit developed areas given that native habitats are available within 1000m.
    - Given this scale-dependent response to development and the negative association of coyote occurrence with increased numbers of vehicles, a development threshold may exist above which coyotes cannot use developing landscapes effectively.
4. The results of the landscape modeling for marten did not indicate significant change in the probability of marten occurrence under 4 development scenarios.
    - This likely reflects the concentration of developable parcels near existing development.
    - This would result in many undeveloped parcels already having a reduced probability of occupancy because of they are surrounded by development above the threshold for marten.
    - Additional information is needed to evaluate the effects of exacerbating the effects of habitat loss at lower elevations and resulting isolation of populations above 7000' elevation.

Assessment

5. Several species and species groups were strongly associated with development and human activity could potentially be used to demonstrate the condition and contribution of native forests in developing areas.
    - A potential indicator of more developed areas would be the occurrence of raccoon
    - Potential indicators of undeveloped conditions include the occurrence of marten, spotted skunk, and bobcat, and more broadly distributed activity patterns (rather than primarily nocturnal).
    - Community level surveys are recommended rather than individual species surveys. Survey duration may need to be extended in developed areas to achieve the same survey-level probability of detection as in less developed areas
6. For the carnivore community, the most important habitat characteristics at the site scale included the volume of coarse woody debris, the occurrence of large and small trees, human activity, and development within 50 m. At the landscape scale, the amounts of meadow and shrub cover were important.

Management

7. Disturbance from human-related activity, particularly dogs, was a negative affector for some species (e.g., rabbits/hares, deer, and black bear).
    - Activity patterns of native carnivores suggested a shift to minimize overlap with temporal periods of greatest dog activity (see Fig. 5.6, 5.7). Human activity and the handling of domestic dogs, particularly implementation and enforcement of leash laws, could reduce potential impacts on native species.
8. Coyotes and raccoons were strongly associated with development and likely benefit from anthropogenic subsidies.
    - Coyotes and raccoons may reach high densities in urban areas leading to conflict with local residents and the potential for disease transmission to domestic pets and people. Reducing access to pet food and garbage and other resources (eg. denning locations) could help reduce densities and the potential for wildlife-human conflict.
    - Coyote populations may warrant monitoring, given that increased abundance of this species could precipitate substantial ecological consequences and elevated conflicts with humans.
9. Black bear populations are changing in response to changes in human population densities and behaviors.
    - Bears are an important component of the ecological and social systems in the basin.
    - A bear management plan for the basin, including monitoring, would be a prudent investment to ensure the health and safety of both bear and human populations.

Future Directions for Research

Remnant forest in developing areas likely plays an important role in the maintenance of carnivore species at lower elevations in the basin. Additional analyses of these data that would be useful for understand the relationship of carnivores to native forest with an urban environment would be a spatial evaluation of the importance of area and configuration to carnivore occurrence.

Further analysis of carnivore activity patterns relative to habitat, development, human activity, and the occurrence of other species (e.g., domestic dogs) would reveal aspects of carnivore behavior that will inform how management can achieve multiple objectives (e.g., forest resources, recreation, wildlife). Further research into bear population demography and behavior in both wildland and urban environments will be needed to inform a bear management plan.

Future studies need to address the impacts of other types of development (e.g., recreational development) on wildlife and wildlife habitat. Recreational development may be of a lower intensity but can impact as large or larger areas than residential development and occurs both at lake level (e.g., golf courses) and at higher elevations (e.g., ski areas) in the basin. Upper montane environments tend to be less productive and, consequently, may be more sensitive to disturbance and slower to respond to perturbation. A study encompassing recreational development and upper montane environments will be particularly important to understanding the response of species such as the marten, whose distributional overlap with lower elevation residential development is moderate to low.

Ants

General

- Ants in the Lake Tahoe basin are a numerically-dominant epigaeic invertebrate that have multi-faceted ecological niches important for ecosystem integrity.
- A total of 32,023 individuals from 46 species were recorded from the 101 sites along the urban development gradient. The richest subfamilies were Formicinae (30 species) and Myrmicinae (13 species).
- Our data illustrate significant species- and community-level responses of ants to the urban development model. They are discussed by management objective below and summarized in Appendix 9.1.

Development

1. Many measures of ant community richness and abundance showed decreases or unimodal relationships with development in the area surrounding forested sites; none showed a strong increase with development.
   - Species richness of ants peaked at approximately 30% of the area within 100 m being developed, demonstrating a unimodal model fit.
   - Total site abundance showed a decline in the maximum abundance by approximately one-third as landscape development (300, 500, and 1000 m) increased.
   - According to species rank-abundance plots, dominance increased with development, but with no apparent threshold, indicating a gradual decline in biological diversity with development. In other words, although high development sites support native fauna, our data indicate that these sites have a greater dominance of a few species, suggesting trends toward biological homogenization.
   - The abundance of log-nesting specialists showed a similar pattern as total abundance, where maximum abundance declined substantially (nearly two-thirds) with development at 100 m, with the decline appearing to drop at around 30% development.
   - The abundance of rare species showed a negative relationship with development at 100 m, with rare species essentially dropping out above 20% developed (all but one species).
2. Individual species responses to development surrounding forested sites included a mix of positive and negative relationships.
   - Eight of 46 species detected and analyzed had strong responses to the development gradient.

- *Formica cf. sibylla* abundance was negatively affected by development at all scales (60 m to 1000 m). This species is likely to be a good indicator of development and associated disturbance.
- *Formica ravida* abundance was consistently positively affected by development across multiple scales. Development explained over 70% of the variance in the abundance of *Formica ravida* at the 60- and 100-m scales of development.
- In high development sites, dominance by *Formica sibylla* was 67.0% to 99.9% greater than any other species, whereas the most dominant species exceeded any other species' abundance by only 6.1% in moderate sites and 1.4% in low development sites.
- The exotic species, *Tetramorium caespitum*, was only observed in high development areas above 60% development.

3. At the site scale, ant community metrics showed a marked negative response to disturbance.
   - Ant species richness appeared to decline as the total area of compacted surface increased from 0 to 2000 m^2 within a 30-m radius area.
   - Ant species richness peaked at moderate levels of site disturbance, consistent with its relationship with development at 100 m.

Assessment

4. A few strong candidate indicators of site conditions were identified in the course of this study.
   - *Formica cf. sibylla* abundance is likely to be a good indicator of development and associated disturbance, given its consistent negative relationship with development.
   - *Formica ravida* abundance is likely to be a good indicator of development and associated disturbance, given its consistent positive relationship with development
   - Total abundance and log-nester abundance both decreased in relation to development within distances of 100 m (and greater). Sites not development are thus predicted to mimic the distribution of abundances observed at undeveloped sites from this study.
   - Community dominance is a good measure of development at the neighborhood scale (within 300 m).
   - Ant species richness appears to be a good indicator of site conditions, declining as sites have increased areas of compacted surface.

Management

5. Minimizing the number and extent of areas where development exceeds 30% at the neighborhood scale (25 to 75 ha, corresponding to 300-m and 500-m radius areas, respectively) would greatly help retain native ant populations and communities.
   - Ant species richness was highest in forests of moderate levels of urban development and low development sites contained many unique species. This indicates that rare species are the first to be lost with progressive development,

followed by the most sensitive species, which are replaced by more tolerant species at moderate levels of development. Losses appeared to accelerate above 20 to 30% development. Specialist abundances also appeared to drop off at 30% development.

- Given that on average single family developments occupy approximately 50% of a parcel, the retention of native vegetation to the extent possible in developed parcels will help keep the total percent of the area developed closer to the target of < 30% developed.
- The retention of undeveloped parcels occupied by native vegetation in urbanizing areas will greatly contribute the keeping the density of development lower, thus reducing the frequency and intensity of impacts occurring when development exceeds 30% of an area.

6. Ant species of concern were identified that should be monitored as development and/or human activity progresses in the lower montane zone.
   - Rare species are clearly at risk from development, and monitoring programs targeting assessment can also be used to monitor the status of rare species. Given the few numbers of rare species in urban forests at the present time (i.e., potential problems of insufficient power to detect trends), the richness or abundance of rare ant species was not considered a strong candidate indicator.
   - Exotic species, like rare species, would be good to monitor in terms of their occurrence and abundance in the course of assessing conditions in urbanizing areas; however, their occurrences are too low to make them strong candidate indicators with sampling methods used in this study.
   - Species-specific sampling methods for exotic and rare species could be developed to more directly gauge distribution and abundance patterns for future monitoring programs.

Future Directions for Research

The research design of this study was aimed at identifying the impacts of urbanization on biological diversity, and we have been successful in describing patterns of community structure and population dynamics with respect to human development. We have also identified species that are potentially vulnerable to development and habitat modification based on their patchy distribution, low observed abundance, and/or specific habitat requirements. However, research is still needed to determine how biodiversity is being affected by specific land management practices as well as how biodiversity changes with elevation; both factors are likely to significantly affect biological diversity in the basin, particularly at lower elevations.

Plants

General

- 387 taxa were observed in 118 sites, including 25 unknowns.
    - The 5 most common species were *Pinus jefferyi*, *Abies concolor*, *Arctostaphylos patula*, *Gayophytum diffusum*, and *Carex rossi*
    - 72% of recorded species were rare (occurring in ≤ 5% of sites)
    - 3% of recorded species were common (occurring in > 50% of sites)
- 41 exotic species were encountered in 36% of sites.
    - The 5 most common exotic species were *Bromus tectorum*, *Dactylis glomerata*, *Taraxicum officinale*, *Elytrigia pontica*, and *Polygonum arenastrum*.
- Relationships between primary measures of the small mammal community and environmental conditions, including human development and activity, are depicted graphically in Appendix 9.1 and discussed in detail below.

Development

1. Plant species richness in native forest fragments increased slightly in response to surrounding development. This was largely driven by nonlinear increases in richness of exotic species. Contrary to expectation, richness of native species was not greatly influenced by development.
    - Richness of exotic species increased along the development gradient.
        - Sites with < 42% development had 0-3 exotic species, while sites with > 42% development had up to 15 exotic species.
        - Development had a positive, nonlinear effect on richness of exotic annual herbs, annual grasses, perennial herbs, and perennial grasses. Sample sizes for exotic shrubs and trees were too small to evaluate these subsets of exotic species.
        - Increases in surrounding development may be associated with more open canopies, which increases the competitive advantage of exotic species and perennial grasses
    - Diversity of native species did not decline with increases in surrounding development
        - Development did not influence species richness of native annual herbs, perennial herbs, shrubs, or trees.
        - Development did not influence average percent cover of native annual herbs, perennial herbs, or shrubs.
        - A decline in average percent cover of native trees with increasing development suggests that urban sites have more open canopies.
        - Development had a positive influence on species richness and average percent cover of native perennial grasses, suggesting that they benefit from the open canopies of urban sites. It is also likely that development is more prevalent in areas with more herbaceous

        understories (i.e., flat, moist areas). Native annual grasses were not detected in the study.
        - As development of surrounding areas increased, the shrubs *Arctostaphylos nevadensis* and *Chrysolepis sempervirens* occurred less frequently, and the native perennial grasses *Festuca idahoensis*, *Poa secunda*, and *Elymus elymoides*; exotic perennial grass *Dactylis glomerata*, and exotic perennial herb *Taraxicum officinale* occurred more frequently. This pattern suggests that exotics and perennial grasses acquire a competitive advantage with increased levels of development, and that the commonly occurring shrubs become less prevalent, potentially as a result of ground disturbance from people.

2. Forest structure within undeveloped forests did not change greatly with increasing surrounding development, with the exception of dead wood (snags and logs), compared to the landscape at large.
    - The living component of forest structure in undeveloped forests was not greatly influenced by increasing surrounding development, especially when compared to the response of developed and undeveloped sites from the landscape at large
        - In undeveloped forests, surrounding development had no impact on shrub cover. In contrast, sites from the landscape at large exhibited lower shrub cover with increasing development.
        - In undeveloped forests, the density and basal area of larger tree size classes were unaffected by level of surrounding development, and there was no effect on height class diversity. In contrast, sites from the landscape at large exhibited lower densities of small and medium trees and lower canopy cover with increasing development, suggesting a shift toward fewer larger trees, a decline in vertical diversity of vegetation in developed areas, and a decline in overall cover.
    - Development had negative impacts on the dead wood component of forest structure in both undeveloped forests and the landscape at large.
        - In undeveloped forests and the landscape at large, increases in surrounding development were associated with fewer, smaller snags with less decay.
        - In undeveloped forests, sites with low to moderate levels of surrounding development had variable amounts of coarse woody debris, while sites with high levels of development consistently had low volumes of coarse woody debris. Although log densities are not available for sites throughout the landscape-at-large, it is likely that they tracked snag densities in that they were even lower in response to development in the landscape-at-large than they were in remnant undeveloped forests.
        - Declines in dead wood were more pronounced outside of undeveloped forests.
    - Undeveloped forests were more heavily managed than forests further from development, as evidenced by a greater number of cut stumps with increasing surrounding development.

3. Decadence features are not correlated with levels of surrounding development
    - Contrary to expectations, disease symptoms were not more common in highly urbanized areas
    - Features of older trees (large cavities, broken tops) were not more prevalent in sites with low levels of surrounding development.

Assessment

4. Forest structure was most readily and frequently altered in remnant forests and developed sites.
    - Key measures of forest structure include tree density by size class (i.e., small, medium, and large diameter trees), snag density by diameter and decay class, log density by diameter class.
5. Exotic plant species richness is an important measure of site conditions as well as success in minimizing the spread of exotic plants.
6. Few native plant species emerged as important indicators of site conditions, but the cover of native shrub species appears to be consistently affected as development and human use increase.

Management

7. Increased levels of development facilitates the invasion of exotic species by altering the habitat to favor shade-intolerant species, increasing input of nutrients, and introducing new species into the environment via foot traffic and vehicles
    - The control and eradication of exotic species in undeveloped forests in more developed areas will serve two important functions.
    - It will reduce the potential spread of exotic plant species into less developed areas by eliminating the ability of remnant forests to serve as stepping stones for establishing exotic plant populations in less developed areas. Edges of larger forest tracts are particularly important focal areas for this work.
    - It will improve the quality of habitat for native plant and animal species within the remnant forest.
    - Exotic species, such as *Bromus tectorum*, *Dactylus glomerata*, *Taraxicum officinale*, *Elytrigia pontina*, and *Lotus corniculatus* should be of particular concern to land managers, because of their abundance and/or invasiveness.
    - Most exotic plant species were escaped ornamentals. Managers could educate and encourage local land owners to plant native or non-invasive ornamental plants to decrease the source of exotics. In addition, xeric landscaping also reduced the ability of some exotic plant species of becoming established.
    - Keeping development < 40% of the landscape will help reduce the frequency of occurrence of exotic plant species. The mitigating activities mentioned above may help keep exotic plant species richness low even where development exceeds the 40% level.
8. Despite increasing levels of surrounding development, undeveloped forest remnants retained many important habitat elements (canopy cover, larger tree density,

vegetation height diversity) that otherwise occur more rarely in a developed landscape.
  - Maintaining undeveloped forest in urbanizing areas contributes ecologically unique and important forest conditions that were shown to support many plant and animal species.
  - Maintaining natural age and size distributions of trees in forests (i.e., smaller diameter trees interspersed with large diameter trees) may help retain habitat quality, particularly for understory associated species of animals.

9. Educating and encouraging private land owners to retain more natural forest structure on their properties will also contribute to the maintenance of biological diversity in more developed areas.
   - Maintaining mature trees clearly has had a positive effect on retaining native forest conditions on developed parcels.
   - Additional efforts could include the retention of some smaller diameter trees, retaining stringers of trees so that higher canopy closures are provided in some areas, and the retention or planting of patches of native shrubs.
   - Providing advice on lot management to achieve wildlife and biodiversity objectives could make a very positive contribution toward maintaining a more connected and ecologically functional landscape in urbanizing areas, particularly since most parcels are not fenced (another important contributor to maintaining landscape function, but not one we studied)..
10. Snags and logs are an important element of forest structure that play a vital role in the ecosystem by providing food substrates and habitat, and contributing to nutrient cycling.
    - Greater retention and restoration of snags and coarse woody debris, particularly larger diameter material (> 60 cm) would be a valuable contribution to maintaining and improving the quality of habitat provided by remnant native forests, particularly in more developed areas.
    - Target snag and log densities could be based on a variety of factors, such as vegetation type and special management objectives.
    - The following guidelines were derived based on the range of conditions observed at undeveloped sample sites.
      - Roughly 50% of remnant undeveloped forests should have > 10 m^3/ha of snags, which is the threshold identified for maintaining bird species richness.
      - This density equates to 12 snags/ha (5 snags/ac) that are > 61 cm (24 in) diameter and > 3.3 m (10 ft) tall, or proportionately fewer per snags ha for larger and/or taller snags (see bird key findings for more details)
      - Of these snags, roughly 80% should be decay class 2 or 3.
      - Roughly one third of remnant undeveloped forests should have > 3 m^2/ha of coarse woody debris and another one third should have > 2 m^2/ha. 1 m^2/ha of coarse wood debris equates to 1 log per ha > 60 cm (24 in) diameter and 3.3 m (10 ft) long, or 5 logs per ha > 28 cm (11 in) diameter and > 3.3 m (10 ft) long.
    - In some instances, snag creation is an option, and it is the only viable option for improving snag and log densities in the near term.

    - Trees that need to be removed because they are dying and pose a threat to people or property may be cut at a height of 10 ft (preferably more) above the ground, creating valuable habitat for snag dependent species while eliminating the risk to people and property.
    - Logs can be created through the same process where some lengths of the tree being removed can be left on the ground, preferably larger diameter sections of the tree.

Future Directions for Research

The focus of this study on remnant native forests limited our ability to describe the full breadth of changes expected as sites are developed. We were able to compare structural conditions in developed and undeveloped sites, but we were not able to compare these two conditions in terms of species composition and cover of herbaceous plants, or to categorize site types into more than two types (developed, undeveloped). Additional insights would be generated by some additional attention to this subject. Insights into the interaction between site and neighborhood development could be derived through additional analysis of existing data. For example, all satellite sites could be classified into one of multiple categories of site development and then reanalyzed to determine how various aspects of forest structure change with site and neighborhood development. Determining effects of different types and levels of site development on non-woody plant composition and structure would require additional field data collection.

A few old growth forest stands remain in the basin, and the characteristics that make then unique relative to other older forests that have been altered by human activities are of keen interest to forest ecologists. In the pursuit of restoration of old forest conditions in the basin, additional understanding as to the unique characteristics missing in older forests that have been altered by human activity, including sites in proximity to various levels of development, would provide helpful guidance to management.

The role of logs in forest nutrient cycling and other forest processes has been studied in other ecosystems and geographic locations; however, it would be informative to know the number and condition of logs that facilitate various functions and processes in basin forests, particularly the facilitation of processes that may be diminished in more disturbed forests.

Soil compaction can greatly change the hydrodynamics of forest sites, which in turn is likely to affect many other forest functions and conditions. Although we did not see strong differences in herbaceous plant composition and structure, we did not obtain sensitive measures of compaction and we only sampled in undeveloped forests. Parcel development is likely to increase compaction of the remaining parcel through various human activities, which may reduce the capacity of the undeveloped portion of the parcel to support a full suite of ecological functions. Additional research into how different types of land uses affect the ability of a site to support its original biological diversity would inform management.

Many of the sites we sampled had been managed at some point in the past, as evidenced by the presence of stumps, and many received fuel treatments soon after we sampled them. The effects of forest management are of great interest to land stewards attempting to meet multiple objectives on public parcels. Since our sampling was designed to address the question of the value of undeveloped sites in a developing landscape, we necessarily avoided other disturbance sources. We were able to identify elements of forest structure and composition that were important determinants of various biodiversity metrics; however we did not directly investigate the question of forest management effects. Some additional insights could be gained from the existing data set by considering the presence and level of management each site experienced. Further insights would require future research by designing a study to address this question directly.

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Appendices

Appendix 2.1 - Richness and abundance of landbird guilds and their responses to development within 300 m of sample units. Data were collected at 75 sample units in the Lake Tahoe basin, 2003-2004. The direction of the effect is negative unless the *P*-value and Adjusted R^2 are in italics. Abundance is the average number of birds detected per point count.

		Richness				Abundance			
Species group	Total # species	Range	Mean ± s.e.	*P*	Adj. R^2	Range	Mean ± s.e.	*P*	Adj. R^2
Nesting groups									
All cavity	15	4-10	8.11 ± 0.17	<0.0001	0.21	1.93-8.54	5.33 ± 0.17	0.0053	0.09
All open	51	10-26	17.67 ± 0.41	<0.0001	0.23	5.43-27.93	12.70 ± 0.43	*0.0033*	*0.10*
Primary cavity exc.	8	1-6	3.53 ± 0.13	0.0009	0.13	0.07-2.13	0.85 ± 0.05	0.0260	0.05
Weak cavity exc.	3	2-3	2.75 ± 0.05	0.1318	0.02	1.43-6.87	3.83 ± 0.13	0.3279	0.00
Secondary cavity	4	0-3	1.83 ± 0.06	0.0035	0.10	0.00-2.00	0.65 ± 0.05	<0.0001	0.36
Ground	13	0-8	3.77 ± 0.22	<0.0001	0.41	0.00-7.87	2.17 ± 0.18	<0.0001	0.36
Shrub	5	0-3	1.31 ± 0.10	0.0001	0.20	0.00-2.47	0.48 ± 0.07	<0.0001	0.31
Tree (overstory)	17	0-11	7.04 ± 0.21	0.0002	0.17	0.00-8.53	3.15 ± 0.20	0.0017	0.11
Tree (understory)	12	3-8	5.04 ± 0.12	*0.9928*	*0.01*	1.40-19.27	6.13 ± 0.37	*<0.0001*	*0.47*
Foraging groups									
Air	8	0-6	2.73 ± 0.17	0.0096	0.08	0.00-16.80	1.67 ± 0.25	*0.2078*	*0.01*
Bark	11	2-8	5.97 ± 0.17	<0.0001	0.28	0.53-5.80	2.62 ± 0.12	0.0005	0.14
Foliage	19	2-14	7.81 ± 0.28	<0.0001	0.21	1.27-8.07	4.93 ± 0.19	<0.0001	0.27
Ground	27	7-14	10.43 ± 0.17	0.3455	0.00	4.07-25.73	10.05 ± 0.44	*<0.0001*	*0.32*
Diet groups									
Granivore	9	1-5	2.79 ± 0.12	0.3452	0.00	0.20-4.07	1.33 ± 0.11	0.9393	0.00
Invertivore	35	8-24	15.63 ± 0.45	<0.0001	0.39	3.00-19.93	9.87 ± 0.32	0.0075	0.08
Nectarivore	2	0-2	0.12 ± 0.04	0.0088	0.08	0.00-0.27	0.01 ± 0.01	0.0174	0.06
Omnivore	20	4-11	7.87 ± 0.16	0.6391	0.01	2.87-20.67	7.80 ± 0.37	*<0.0001*	*0.36*
All landbirds	68	16-37	27.07 ± 0.51	<0.0001	0.33	7.57-34.47	19.32 ± 0.50	*0.0159*	*0.06*

Appendix 2.2 - Richness and abundance of landbird families and their responses to development within 300 m of sample units. Data were collected at 75 sample units in the Lake Tahoe basin, 2003-2004. The direction of the effect is negative unless the *P*-value and Adjusted R^2 are in italics.

		Richness				Abundance			
Bird family	Total # species	Range	Mean ± s.e.	*P*	Adj. R^2	Range	Mean ± s.e.	*P*	Adj. R^2
Columbidae (pigeons and doves)	2	0-2	1.56 ± 0.06	*0.0017*	*0.11*	0.00-4.13	0.65 ± 0.08	*0.0003*	*0.15*
Corvidae (jays and crows)	5	1-3	1.84 ± 0.08	0.4743	0.01	0.60-6.33	3.18 ± 0.18	*<0.0001*	*0.50*
Embezeridae (sparrows)	8	0-6	2.59 ± 0.11	0.0001	0.17	0.00-5.40	1.79 ± 0.12	<0.0001	0.26
Fringillidae (finches)	8	0-5	2.51 ± 0.13	0.5861	0.01	0.00-5.33	1.12 ± 0.12	0.4245	0.00
Hirundinidae (swallows)	3	0-3	0.68 ± 0.09	*<0.0001*	*0.28*	0.00-16.80	0.70 ± 0.25	*0.0001*	*0.18*
Icteridae (blackbirds)	4	0-4	1.79 ± 0.09	*<0.0001*	*0.37*	0.00-13.40	2.43 ± 0.29	*<0.0001*	*0.29*
Parulidae (wood-warblers)	6	0-5	2.17 ± 0.15	<0.0001	0.21	0.00-4.07	1.04 ± 0.10	<0.0001	0.35
Picidae (woodpeckers)	8	1-6	3.53 ± 0.13	0.0009	0.13	0.07-2.13	0.85 ± 0.05	0.0260	0.05
Sittidae (nuthatches)	3	1-3	2.47 ± 0.08	0.0013	0.12	0.13-3.93	1.77 ± 0.09	0.1216	0.02
Trochilidae (hummingbirds)	2	0-1	0.11 ± 0.04	0.0074	0.08	0.00-0.27	0.01 ± 0.01	0.0174	0.06
Turdidae (thrushes)	3	1-3	1.57 ± 0.09	<0.0001	0.30	0.13-3.33	1.21 ± 0.07	*0.0082*	*0.08*
Tyrannidae (tyrant flycatchers)	3	0-3	1.60 ± 0.12	<0.0001	0.31	0.00-4.73	0.89 ± 0.11	<0.0001	0.35
Vireonidae (vireos)	2	0-2	0.75 ± 0.09	<0.0001	0.26	0.00-1.53	0.22 ± 0.04	<0.0001	0.20
All landbirds	68	16-37	27.07 ± 0.51	<0.0001	0.33	7.57-34.47	19.32 ± 0.50	*0.0159*	*0.06*

Appendix 2.3 - Abundance of selected landbird species and their responses to development within 300 m of sample units. Data were collected at 75 sample units in the Lake Tahoe basin, 2003-2004.

Common name	Scientific name	Range	Mean ± s.e.	Relationship[1]	*P*	Adj. R^2
Open nesters						
American Robin	*Turdus migratorius*	0.00-3.33	1.04 ± 0.08	+	<0.0001	0.28
Hermit Thrush		0.00-1.53	0.09 ± 0.03	-	0.0004	0.15
Steller's Jay	*Cyanocitta stelleri*	0.60-6.33	2.98 ± 0.18	+	<0.0001	0.45
Dusky Flycatcher	*Empidonax oberholseri*	0.00-2.13	0.30 ± 0.06	-	<0.0001	0.35
Western Wood-pewee		0.00-3.53	0.46 ± 0.07	-	0.0331	0.05
Dark-eyed Junco	*Junco hyemalis*	0.00-2.27	0.92 ± 0.06	-	0.0005	0.14
Olive-sided Flycatcher		0.00-1.20	0.13 ± 0.03	-	0.0026	0.11
Brewer's Blackbird		0.00-7.93	1.07 ± 0.20	+	<0.0001	0.28
Cliff Swallow		0.00-16.40	0.61 ± 0.24	+	0.0002	0.16
Hermit Warbler		0.00-0.87	0.03 ± 0.01	-	0.0079	0.08
Townsend's Solitaire		0.00-0.73	0.08 ± 0.02	-	<0.0001	0.22
Western Tanager		0.00-1.67	0.57 ± 0.05	-	<0.0001	0.27
Yellow-rumped Warbler		0.00-1.87	0.69 ± 0.06	-	<0.0001	0.23
Cavity nesters						
White-headed Woodpecker	*Picoides albolarvatus*	0.00-0.87	0.19 ± 0.02	0	0.3902	0.00
Hairy Woodpecker	*Picoides villosus*	0.00-0.73	0.18 ± 0.02	-	<0.0001	0.31
Pileated Woodpecker		0.00-0.20	0.01 ± 0.00	-	0.0050	0.09
Northern Flicker	*Colaptes auratus*	0.00-1.00	0.33 ± 0.03	0	0.8182	0.00
Pygmy Nuthatch	*Sitta pygmaea*	0.00-3.33	0.85 ± 0.09	+	0.0002	0.17
Red-breasted Nuthatch	*Sitta canadensis*	0.00-2.73	0.69 ± 0.08	-	<0.0001	0.31
White-breasted Nuthatch	*Sitta*	0.00-1.13	0.23 ± 0.03	-	0.0001	0.17
Brown Creeper	*Certhia americana*	0.00-1.13	0.37 ± 0.03	-	<0.0001	0.34
Mountain Chickadee	*Poecile gambeli*	0.47-4.07	2.29 ± 0.08	0	0.2616	0.00
Other						
Brown-headed Cowbird	*Molothrus ater*	0.00-3.60	1.29 ± 0.09	+	<0.0001	0.25

[1] "+" = positive; "-" = negative; "0" = no relationship

Appendix 2.4 - Daily survival rates of nests, using the Mayfield method (Mayfield 1975), as amended (Hensler and Nichols 1981, Bart and Robson 1982).

Species or species group	Development category	No. nests[1]	Daily survival rate	s.e.	Trans. survival rate[2]	s.e.
Comparisons among species groups						
Cavity nesters	All	239	0.9934	0.0014	0.1448	0.0156
Ground open nesters	All	33	0.9418	0.0151	0.3816	0.0471
Tree and shrub open nesters	All	144	0.9788	0.0034	0.2527	0.0198
All open nesters	All	177	0.9745	0.0035	0.2742	0.0183
Primary cavity excavators	All	68	0.9961	0.0019	0.1132	0.0281
Weak and secondary cavity excavators	All	171	0.9921	0.0019	0.1571	0.0188
Within-group comparisons between development categories						
All species	High	154	0.9889	0.0023	0.1820	0.0191
	Low	262	0.9841	0.0022	0.2226	0.0152
Cavity nesters	High	84	0.9965	0.0018	0.1045	0.0259
	Low	155	0.9916	0.0020	0.1636	0.0196
All open nesters	High	70	0.9788	0.0049	0.2457	0.0281
	Low	107	0.9714	0.0048	0.2938	0.0240
Primary cavity excavators	High	24	0.9942	0.0040	0.1344	0.0469
	Low	44	0.9970	0.0021	0.0997	0.0351
Weak exc. and secondary cavity nest.	High	60	0.9975	0.0018	0.0885	0.0311
	Low	111	0.9889	0.0029	0.1859	0.0236
American Robin	High	37	0.9824	0.0058	0.2257	0.0368
	Low	27	0.9863	0.0068	0.2012	0.0491
Mountain Chickadee	High	26	0.9963	0.0037	0.1022	0.0508
	Low	49	0.9818	0.0057	0.2269	0.0348
Pygmy Nuthatch	High	22	1.0000	0.0000	-	-
	Low	32	0.9915	0.0042	0.1650	0.0406
Within-group comparisons by development and use categories						
All species	High, high[3]	88	0.9915	0.0027	0.1583	0.0247
	High, low	66	0.9851	0.0043	0.2127	0.0300
	Low, high	101	0.9918	0.0025	0.1596	0.0238
	Low, low	161	0.9787	0.0033	0.2586	0.0197
Cavity nesters	High, high	50	0.9969	0.0022	0.0961	0.0338
	High, low	34	0.9958	0.0029	0.1156	0.0405
	Low, high	67	0.9958	0.0021	0.1167	0.0290
	Low, low	88	0.9880	0.0033	0.1952	0.0266
All open nesters	High, high	38	0.9848	0.0053	0.2092	0.0363
	High, low	32	0.9690	0.0096	0.2945	0.0445
	Low, high	34	0.9822	0.0067	0.2255	0.0415
	Low, low	73	0.9660	0.0064	0.3244	0.0294

[1] The number of nests in the sample. Of this total, only nests with at least two visits are included; nests with a single visit have no intervals and thus a daily survival rate cannot be calculated.

[2] The transformed survival rate is the daily survival rate transformed to be normally distributed. This is the value used by program CONTRAST (Hines and Sauer 1989) to compare survival rates.

[3] The first category is development; the second, use.

Appendix 3.1. Full models of small mammal species richness for each explanatory factors group. Individual factors are listed for each group, with the direction of the relationship with species richness indicated as positive '+' or negative '**-**' based on the parameter estimates. AIC_C values that adjust for small sample sizes were used to rank models for comparison, and the models are listed from lowest to highest AIC_C. Also presented are the number of model parameters (**k**), model likelihood, model weight (**Wi**), R^2, adjusted R^2 (**Adj-R^2**), and the model p-value.

Explanatory factors group: Parameters	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Development at 1000m: +Year03-04, - Julian, +Development	3	69.02	69.95	0	1	0.27	18.57%	12.30%	0.0180
Development at 300m: +Year03-04, - Julian, +Development	3	69.28	70.21	0.26	0.88	0.24	18.27%	11.98%	0.0198
Disturbance: +Year03-04, - Julian, - Spatial location, + People/hr, + dogs/hr	4	69.41	70.72	0.77	0.68	0.18	21.62%	14.28%	0.0134
Development at 100m: +Year03-04, - Julian, - Development	3	70.42	71.34	1.40	0.50	0.13	16.95%	10.56%	0.0304
Predators: +Year03-04, + Domestic dogs, - Domestic cats, - Native predator species richness	5	70.53	72.31	2.36	0.31	0.08	23.80%	15.33%	0.0130
Vegetation ground: +Year03-04, - Julian, - Grasses, + Herbs, + Shrubs, + Bare ground, - Rock, - Litter, + CWD	9	73.20	77.67	7.72	0.02	0.01	33.80%	21.46%	0.0063
Abiotic: +Year03-04, -Year03-05, - Julian, - Spatial location, - Elevation, + Slope, - Precipitation	5	75.99	77.77	7.82	0.02	0.01	17.71%	8.56%	0.0784
Habitat types 100m: +Year03-04, -Year03-05, - Julian, + Habitat heterog, + Aspen, + Coniferous forest, - Grassland, + Montane riparian, + Shrubland	9	74.59	78.25	8.31	0.02	0.00	29.39%	17.62%	0.0141
Vegetation canopy: +Year03-04, - Julian, - % Cover trees, + Trees12-27, + Trees 28-60, + Trees60, + Snags	7	75.80	78.75	8.80	0.01	0.00	24.88%	13.80%	0.0306
Habitat types 300m: +Year03-04, - Julian, + Habitat heterog., + Aspen, - Barren, + Conifer forest, + Grassland, + Montane riparian, - Shrubland	9	80.20	84.68	14.73	0.00	0.00	26.93%	13.31%	0.0472
Habitat types 500m: +Year03-04, - Julian, + Habitat heterogeneity, + Aspen, + Barren, + Coniferous forest, + Grassland, - Montane riparian, + Shrubland	9	81.97	86.44	16.49	0.00	0.00	25.10%	11.13%	0.0749

Appendix 3.2. Model equations for the top ranked reduced models of small mammal species richness for each explanatory factors group. AIC$_C$ values that adjust for small sample sizes were used to rank models for comparison. Also presented are the number model parameters (**k**), model likelihood, R^2 and adjusted R^2 (**Adj-R^2**) values and the p-value of the model. A key to the parameter abbreviations is at the bottom of the page.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Vegetation ground: 5.15 + 0.647**BR**	1	58.99	59.05	0	1	0.5232	15.99%	14.77%	0.0005
CWHR Habitat types 300m: 4.75 + 1.01**Y3-4** – 0.354**JUL** + 0.453**HH300**	3	60.35	60.71	1.65	0.4373	0.2288	21.23%	17.70%	0.0001
Development at 1000m: 4.75 + 1.01**Y3-4** – 0.371**JUL** + 0.155**D1000**	3	63.29	63.65	4.60	0.1005	0.0526	14.43%	10.60%	0.0146
Disturbance: 4.74 + 1.04**Y3-4** – 0.360**JUL** + 0.341**P/H**	3	63.43	63.79	4.73	0.0937	0.0490	17.93%	14.25%	0.004
CWHR Habitat types 100m: 5.15 + 0.511**HH100**	1	63.91	63.97	4.92	0.0855	0.0447	9.97%	8.66%	0.0073
Predators: 4.82 + 0.947**Y3-4** – 0.306**JUL** – 0.236**LOC** + 0.402**CAFA**	4	63.53	64.14	5.09	0.0786	0.0411	21.28%	16.51%	0.003
CWHR Habitat types 500m: 4.77 + 0.967**Y3-4** + 0.358**HH500**	2	64.70	64.88	5.82	0.0544	0.0285	12.78%	10.21%	0.0096
Vegetation canopy: 4.77 + 0.997**Y3-4** – 0.36**JUL** – 0.439**%TR** + 0.374**CT12-27** + 0.299**CT60**	5	65.54	66.46	7.41	0.0246	0.0129	22.47%	16.51%	0.0047
Development at 300m: 4.76 + 0.993**Y3-4** – 0.384**JUL** + 0.129**D300**	3	66.61	66.97	7.92	0.0191	0.0100	14.16%	10.32%	0.0161
Development at 100m: 4.75 + 1.01**Y3-4** – 0.383**JUL** + 0.024**D300**	3	67.12	67.48	8.43	0.0148	0.0077	13.54%	9.64%	0.0202
Abiotic: 4.96 + 0.769**Y3-4** – 0.578**Y3-5** – 0.366**JUL** – 0.282**LOC** – 1.78**PRE**	5	69.79	70.72	11.66	0.0029	0.0015	17.68%	11.35%	0.024

Key to model parameters **ASP#**: % cover of aspen habitat within ‘#’ meters; **BR**: % cover bare ground; **CF#**: % cover of coniferous forest within ‘#’ meters; **D#**: % developed within ‘#’ meters; **GR#**: % cover of grassland within ‘#’ meters; **HH#**: habitat heterogeneity within ‘#’ meters; **JUL**: Julian sampling date; **LOC**: spatial location; **MR#**: % cover of montane riparian within ‘#’ meters; **P/H**: people/hr; **SH#**: % cover of shrubland within ‘#’ meters; **Y3-4**: year 2004 relative to 2003; **Y3-5**: year 2005 relative to 2003.

Appendix 3.3. Full models of the total relative abundance of all small mammal species for each explanatory factors group. Individual factors are listed for each group, with the direction of the relationship with abundance indicated as positive ‘+’ or negative ‘-’ based on the parameter estimates. AIC_C values that adjust for small sample sizes were used to rank models for comparison, and the models are listed from lowest to highest AIC_C. Also presented are the number of model parameters (**k**), model likelihood, model weight (**Wi**), R^2, adjusted R^2 (**Adj-R^2**), and the model p-value.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Vegetation ground: +Year03-04, - Julian, - Grasses, - Herbs, - Shrubs, + Bare ground, - Rock, - Litter, + CWD	9	-344.30	-341.34	0	1	0.7216	52.13%	45.07%	<0.0001
Development at 300m: +Year03-04, - Julian, +Development	3	-338.97	-338.61	2.73	0.2554	0.1843	32.93%	29.92%	<0.0001
Development at 1000m: +Year03-04, - Julian, +Development	3	-337.34	-336.99	4.36	0.1132	0.0817	31.37%	28.29%	<0.0001
Development at 100m: +Year03-04, - Julian, - Development	3	-332.51	-332.15	9.20	0.0101	0.0073	26.19%	23.19%	0.0001
Habitat types 500m: +Year03-04, - Julian, - Habitat heterog., - Aspen, + Barren, - Conifer forest, - Grassland, - Montane riparian, - Shrubland	9	-333.38	-330.43	10.91	0.0043	0.0031	44.17%	35.94%	<0.0001
Habitat types 300m: +Year03-04, - Julian, + Habitat heterogeneity, - Aspen, + Barren, - Coniferous forest, - Grassland, - Montane riparian, - Shrubland	9	-330.63	-327.68	13.66	0.0011	0.0008	41.98%	33.42%	<0.0001
Abiotic: +Year03-04, - Julian, - Elevation, + Slope, - Precipitation	5	-327.51	-326.59	14.76	0.0006	0.0005	27.71%	22.14%	0.0006
Predators: +Year03-04, - Julian, + Domestic dogs, + Domestic cats, - Native predator species richness	5	-327.51	-326.59	14.76	0.0006	0.0005	27.65%	22.09%	0.0001
Habitat types 100m: +Year03-04, - Julian, + Habitat heterogeneity, - Aspen, - Coniferous forest, - Grassland, - Montane riparian, - Shrubland	8	-327.88	-325.56	15.78	0.0004	0.0003	36.87%	28.75%	0.0002
Vegetation canopy: +Year03-04, - Julian, - % Cover trees, + Trees12-27, + Trees 28-60, - Trees60, - Snags	7	-324.17	-322.39	18.95	0.0001	0.0001	30.55%	22.83%	0.0012
Disturbance: +Year03-04, - Julian, + People/hr, + Dogs/hr	4	-322.61	-322.00	19.34	0.0001	0.0000	19.07%	14.17%	0.0068

Appendix 3.4. Model equations for the top ranked reduced models of small mammal relative abundance for each explanatory factors group. AIC$_C$ values that adjust for small sample sizes were used to rank models for comparison. Also presented are the number model parameters (**k**), model likelihood, R^2 and adjusted R^2 (**Adj-R^2**) values and the p-value of the model. A key to the parameter abbreviations is at the bottom of the page.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Vegetation ground: 0.179 + 0.057**BR** – 0.020**HB** – 0.014**RK** – 0.016**LR** – 0.017**CWD**	5	-351.83	-350.91	0	1	0.9901	48.67%	44.72%	<0.0001
CWHR Habitat types 500m: 0.162 + 0.044**Y3-4** – 0.020**JUL** – 0.094**CF500** – 0.040**SH500** – 0.036**GR500** – 0.025**ASP500**	6	-340.70	-339.39	11.52	0.0031	0.0031	42.53%	37.14%	<0.0001
Habitat types 300m: 0.159 + 0.051**Y3-4** – 0.018**JUL** – 0.065**CF300** – 0.024**GR300** – 0.024**ASP300**	5	-340.09	-339.17	11.74	0.0028	0.0028	39.38%	34.73%	<0.40001
Development at 300m: 0.161 – 0.047**Y3-4** – 0.031**JUL** + 0.047**D300**	3	-338.97	-338.61	12.29	0.0021	0.0021	32.93%	29.92%	<0.0001
Development at 1000m: 0.159 + 0.053**Y3-4** – 0.027**JUL** + 0.045**D1000**	3	-337.34	-336.99	13.92	0.0009	0.0009	31.37%	28.29%	<0.0001
CWHR Habitat types 100m: 0.164 + 0.038**Y3-4** – 0.023**JUL** + 0.022**HH100** – 0.037**CF100**	4	-336.88	-336.28	14.63	0.0007	0.0007	33.77%	29.76%	<0.0001
Vegetation canopy: 0.157 – 0.058**Y3-4** – 0.029**JUL** – 0.041**SN**	3	-333.69	-333.33	17.58	0.0002	0.0002	27.70%	24.47%	<0.0001
Development at 100m: 0.161 + 0.048**Y3-4** – 0.036**JUL** + 0.039**D100**	3	-332.51	-332.15	18.76	0.0001	0.0001	26.19%	23.19%	0.0001
Predators: 0.159 + 0.049**Y3-4** + 0.035**CAFA** – 0.035**NSP**	4	-330.59	-329.98	20.92	0.0000	0.0000	27.65%	23.27%	0.0002
Abiotic: 0.161 + 0.047**Y3-4** – 0.031**JUL** – 0.032**PRE**	3	-328.84	-328.49	22.42	0.0000	0.0000	22.58%	19.11%	0.0006
Disturbance: 0.158 + 0.055**Y3-4** – 0.029**JUL** + 0.025**P/H**	3	-325.44	-325.08	25.83	0.0000	0.0000	18.75%	15.11%	0.0029

Key to model parameters **ASP#**: % cover of aspen habitat within '#' meters; **BR**: % cover bare ground; **CAFA**: domestic dog presence; **CF#**: % cover of coniferous forest within '#' meters; **CWD**; est. volume of coarse woody debris; **D#**: % developed within '#' meters; **GR#**: % cover of grassland within '#' meters; **HB**: % cover of herbs; **HH#**: habitat heterogeneity within '#' meters; **JUL**: Julian sampling date; **LOC**: spatial location; **LR**; % cover of litter; **MR#**: % cover of montane riparian habitat within '#' meters; **NSP**: native predator species richness; **P/H**: people/hr; **PRE**: precipitation; **RK**; % cover of rocks; **SH#**: % cover of shrubland within '#' meters; **SN**: % cover of snags; **Y3-4**: year 2004 relative to 2003.

Appendix 3.5. Full models of the total relative abundance of arboreal squirrels for each explanatory factors group. Individual factors are listed for each group, with the direction of the relationship with squirrel abundance indicated as positive ‘+’ or negative ‘-’ based on the parameter estimates. AIC_C values that adjust for small sample sizes were used to rank models for comparison, and the models are listed from lowest to highest AIC_C. Also presented are the number of model parameters (**k**), model likelihood, model weight (**Wi**), R^2, adjusted R^2 (**Adj-R^2**), and the model p-value.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p**
Development at 1000m: +Year03-04, - Spatial location, +Development	3	-588.86	-588.50	0	1	0.8416	16.26	12.51	0.0075
Development at 300m: +Year03-04, - Spatial location, +Development	3	-584.30	-583.95	4.56	0.1025	0.0862	10.47	6.46	0.0585
Predators: +Year03-04, - Spatial location, + Domestic dogs, + Domestic cats, - Native predator species richness	5	-583.77	-582.85	5.65	0.0592	0.0498	17.28	10.92	0.0273
Development at 100m: +Year03-04, - Spatial location, +Development	3	-580.91	-580.55	7.95	0.0187	0.0158	6.08	1.87	0.2374
Abiotic: +Year03-04, - Spatial location, - Elevation, - Slope, - Precipitation	5	-578.68	-577.76	10.74	0.0047	0.0039	11.14	4.30	0.1648
Disturbance: +Year03-04, - Spatial location, + People/hr, + Dogs/hr	4	-577.50	-576.89	11.61	0.0030	0.0025	5.63	-0.09	0.4226
Vegetation ground: +Year03-04, - Spatial location, - Grasses, + Herbs, - Shrubs, + Bare ground, - Rock, - Litter, + CWD	9	-572.62	-569.67	18.83	0.0001	0.0001	18.85	6.88	0.1434
Vegetation canopy: +Year03-04, - Spatial location, + % Cover trees, + Trees12-27, + Trees 28-60, + Trees60, - Snags	7	-570.39	-568.62	19.89	0.0000	0.0000	8.50	-1.66	0.5614
Habitat types 100m: +Year03-04, - Spatial location, + Habitat heterogeneity, +(Habitat heterogeneity^2), +Aspen, - Montane chaparral, + Montane riparian, + Perennial grassland, - Red fir/Subalpine conifer, - Sierran mixed conifer/White fir	10	-570.91	-567.24	21.26	0.0000	0.0000	20.50	7.26	0.1452
Habitat types 500m: +Year03-04, - Spatial location, + Habitat heterogeneity, - (Habitat heterogeneity^2), +Aspen, - Barren, + Lodgepole pine, - Montane chaparral/Sagebrush, + Montane riparian/Wet meadow, + Perennial grassland, - Red fir/Subalpine conifer, - Sierran mixed conifer/White fir	12	-560.06	-554.68	33.82	0.0000	0.0000	15.37	-2.14	0.5734
Habitat types 300m:	12	-559.18	-553.80	34.70	0.0000	0.0000	14.31	-3.42	0.6419

Explanatory Factors Group: Model equation	k	AIC	AICc	ΔAICc	Model likelihood	Wi	R^2	Adj - R^2	p
+Year03-04, - Spatial location, + Habitat heterogeneity, - (Habitat heterogeneity^2), -Aspen, - Barren, + Lodegpole pine, + Montane chaparral/Sagebrush, + Montane riparian/Wet meadow, + Perennial grassland, - Red fir/Subalpine conifer, - Sierran mixed conifer/White fir									

Appendix 3.6. Model equations for the top ranked reduced models of total relative abundance of arboreal squirrels for each explanatory factors group. AIC$_C$ values that adjust for small sample sizes were used to rank models for comparison. Also presented are the number model parameters (**k**), model likelihood, R^2 and adjusted R^2 (**Adj-R^2**) values and the p-value of the model. A key to the parameter abbreviations is at the bottom of the page.

Explanatory Factors Group: Model equation	k	AIC	AICc	ΔAICc	Model likelihood	Wi	R^2	Adj - R^2	p-value
Predators: 0.014 + 0.006**CAFA**	1	-591.71	-591.66	0	1	0.3946	12.12%	10.84%	9.51
CWHR Habitat types 100m: 0.013 + 0.005**HH100**	1	-591.66	-591.60	0.06	0.9715	0.3834	12.05%	10.77%	9.45
Development at 1000m: 0.013 + 0.005**D1000**	1	-588.65	-588.59	3.07	0.2158	0.0851	8.24%	6.91%	6.19
Vegetation ground: 0.013 – 0.004**RK**	1	-587.63	-587.58	4.08	0.1301	0.0513	6.92%	5.57%	5.13
Abiotic: 0.011 + 0.006**Y3-4** – 0.004**EL**	2	-586.58	-586.40	5.26	0.0722	0.0285	9.48%	6.82%	3.55
CWHR Habitat types 500m: 0.131 + 0.003**MCP_SGB500**	1	-585.93	-585.87	5.78	0.0556	0.0219	4.61%	3.23%	3.33
Development 300m: 0.0131 – 0.003**D300**	1	-585.39	-585.33	6.33	0.0423	0.0167	3.93%	2.53%	2.82
CWHR Habitat types 300m: 0.011 + 0.006**Y3-4** + 0.003**HH300**	2	-584.03	-583.85	7.80	0.0202	0.0080	6.18%	3.42%	2.24
Development at 100m: 0.0131 + 0.001**D100**	1	-582.89	-582.83	8.83	0.0121	0.0048	0.49%	-0.96%	0.34
Vegetation canopy: 0.011 + 0.006**Y3-4** – 0.002**SN**	2	-582.80	-582.62	9.04	0.0109	0.0043	4.53%	1.72%	1.61
Disturbance: 0.011 + 0.006**Y3-4** – 0.002**LOC** + 0.001**P/H**	3	-580.54	-580.19	11.47	0.0032	0.0013	5.60%	1.37%	1.32

Key to model parameters **CAFA**: domestic dog presence; **D#**: % developed within '#' meters; **EL**: elevation **HH#**: habitat heterogeneity within '#' meters; **LOC**: spatial location; **MCP_SGB#**: % cover of montane chaparral/sagebrush habitat within '#' meters; **P/H**: people/hr; **RK**; % cover of rocks; **SN**: % cover of snags; **Y3-4**: year 2004 relative to 2003.

Appendix 3.7. Full models of the total relative abundance of terrestrial granivores (ground squirrels and chipmunks) for each explanatory factors group. Individual factors are listed for each group, with the direction of the relationship with terrestrial granivore abundance indicated as positive '+' or negative '-' based on the parameter estimates. AIC_C values that adjust for small sample sizes were used to rank models for comparison, and the models are listed from lowest to highest AIC_C. Also presented are the number of model parameters (**k**), model likelihood, model weight (**Wi**), R^2, adjusted R^2 (**Adj-R^2**), and the model p-value.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Vegetation ground: +Year03-04, - Julian, - Grasses, + Herbs, - Shrubs, + Bare ground, - Rock, - Litter, - CWD	9	-357.05	-354.10	0	1	0.9947	53.69%	46.85%	<0.0001
Development at 1000m: +Year03-04, - Julian, +Development, + (Development^2)	4	-342.89	-342.28	11.82	0.0027	0.0027	29.54%	25.27%	0.00010
Development at 300m: +Year03-04, - Julian, +Development, - (Development^2)	4	-342.19	-341.59	12.52	0.0019	0.0019	28.83%	24.52%	0.00010
Development at 100m: +Year03-04, - Julian, +Development	3	-338.82	-338.46	15.64	0.0004	0.0004	22.16%	18.68%	0.00070
Abiotic: +Year03-04, - Julian, - Elevation, + Slope, - Precipitation	5	-338.63	-337.71	16.39	0.0003	0.0003	28.32%	22.81%	0.00050
Predators: +Year03-04, - Julian, + Domestic dogs, + Domestic cats, - Native predator species richness	5	-333.88	-332.96	21.14	0.0000	0.0000	23.41%	17.52%	0.00330
Disturbance: +Year03-04, - Julian, + People/hr, + Dogs/hr	4	-333.14	-332.54	21.57	0.0000	0.0000	19.10%	14.19%	0.00670
Vegetation canopy: +Year03-04, - Julian, - % Cover trees, + Trees12-27, + Trees 28-60, - Trees60, - Snags	7	-333.87	-332.09	22.01	0.0000	0.0000	29.79%	21.99%	0.00160
Habitat types 100m: +Year03-04, - Julian, + Habitat heterogeneity, - (Habitat heterogeneity^2), - Aspen, + Montane chaparral, - Montane riparian, - Perennial grassland, - Red fir/Subalpine conifer, - Sierran mixed conifer/White fir	10	-328.06	-324.39	29.71	0.0000	0.0000	33.30%	22.18%	0.00400
Habitat types 300m: +Year03-04, - Julian, + Habitat heterogeneity, - (Habitat heterogeneity^2), -Aspen, + Barren, - Lodegpole pine, + Montane chaparral/Sagebrush, + Montane riparian/Wet meadow, - Perennial grassland, - Red fir/Subalpine conifer, - Sierran mixed conifer/White fir	12	-321.89	-316.51	37.59	0.0000	0.0000	33.50%	19.74%	0.01220

Explanatory Factors Group: Model equation	k	AIC	AICc	ΔAICc	Model likelihood	Wi	R^2	Adj - R^2	p-value
Habitat types 500m: +Year03-04, - Julian, + Habitat heterogeneity, - (Habitat heterogeneity^2), -Aspen, + Barren, - Lodegpole pine, + Montane chaparral/Sagebrush, - Montane riparian/Wet meadow, + Perennial grassland, - Red fir/Subalpine conifer, - Sierran mixed conifer/White fir	12	-315.60	-310.22	43.88	0.0000	0.0000	27.39%	12.37%	0.06540

Appendix 3.8. Model equations for the top ranked reduced models of total relative abundance of terrestrial granivores for each explanatory factors group. AIC$_C$ values that adjust for small sample sizes were used to rank models for comparison. Also presented are the number model parameters (**k**), model likelihood, R^2 and adjusted R^2 (**Adj-R^2**) values and the p-value of the model. A key to the parameter abbreviations is at the bottom of the page.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Vegetation ground: 0.158 - 0.026**HB** + 0.066**BR**	2	-371.76	-371.58	0	1	1.0000	48.79%	47.28%	<0.0001
Development at 300m: 0.142 + 0.039**Y3-4** – 0.032**JUL** – 0.034**D300**	3	-342.25	-341.89	29.69	0.0000	0.0000	25.68%	22.36%	0.00020
Development at 1000m: 0.141 + 0.043**Y3-4** – 0.029**JUL** + 0.032**D1000**	3	-341.20	-340.85	30.73	0.0000	0.0000	24.61%	21.23%	0.00030
CWHR Habitat types 100m: 0.158 – 0.028**JUL** + 0.032**MCP_SGB100**	2	-339.88	-339.71	31.87	0.0000	0.0000	19.80%	17.44%	0.00060
Abiotic: 0.143 0.038**Y3-4** 0.032**JUL** – 0.029**PRE**	3	-339.89	-339.54	32.04	0.0000	0.0000	23.20%	19.76%	0.00050
Vegetation canopy: 0.139 0.048**Y3-4** – 0.026**JUL** – 0.036**SN**	3	-343.21	-342.86	28.72	0.0000	0.0000	26.69%	23.41%	0.00010
Development at 100m: 0.142 + 0.039**Y3-4** – 0.035**JUL** + 0.028**D100**	3	-338.82	-338.46	33.12	0.0000	0.0000	22.16%	18.68%	0.00070
Predators: 0.141 + 0.040**Y3-4** – 0.031**JUL** + 0.022**CAFA** – 0.029**NSP**	4	-337.06	-336.46	35.12	0.0000	0.0000	23.40%	18.76%	0.00130
CWHR Habitat types 500m: 0.141 + 0.042**Y3-4** – 0.033**JUL** – 0.022**SMC_WFR500**	3	-336.02	-335.66	35.92	0.0000	0.0000	18.88%	15.25%	0.00270
Disturbance: 0.140 + 0.045**Y3-4** – 0.031**JUL** + 0.022**P/H**	3	-335.93	-335.57	36.01	0.0000	0.0000	18.78%	15.14%	0.00290
CWHR Habitat types 300m: 0.158 – 0.026**JUL** + 0.023**MCP_SGB300**	2	-335.60	-335.42	36.16	0.0000	0.0000	14.90%	12.39%	0.00420

Key to model parameters **BR**: % cover bare ground; **CAFA**: domestic dog presence; **D#**: % developed within '#' meters; **HB**: % cover of herbs; **JUL**: Julian sampling date; **MCP_SGB#**: % cover of montane chaparral/Ssgebrush habitat within '#' meters; **NSP**: native predator species richness; **P/H**: people/hr; **SMC_WFR#**: % cover of Sierran mixed conifer/white fir habitat within '#' meters; **SN**: % cover of snags; **Y3-4**: year 2004 relative to 2003.

Appendix 3.9. Full models of the total relative abundance of terrestrial herbivores (voles and jumping mice). Individual factors are listed for each group, with the direction of the relationship with terrestrial herbivore abundance indicated as positive ‘+’ or negative ‘-’ based on the parameter estimates. AIC_C values were used to rank models for comparison. Also presented are the number of model parameters (**k**), model likelihood, model weight (**Wi**), R^2, adjusted R^2 (**Adj-R^2**), and the model p-value.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Development at 300m: +Year03-04, +Year03-05, + Julian, + Spatial location, + Dev, + (Dev^2)	6	-582.37	-581.05	0	1	0.9915	41.79%	36.33%	<0.0001
Development at 100m: +Year03-04, +Year03-05, + Julian, + Spatial location, + Development	5	-571.65	-570.72	10.33	0.0057	0.0057	29.64%	24.23%	0.0003
Development at 1000m: +Year03-04, +Year03-05, + Julian, + Spatial location, + Dev, + (Dev^2)	6	-570.61	-569.30	11.76	0.0028	0.0028	31.52%	25.10%	0.0003
Predators: +Year03-04, +Year03-05, + Julian, + Spatial location, + Domestic dogs, - Domestic cats, - Native predator species richness	7	-561.18	-559.40	21.65	0.0000	0.0000	25.16%	16.84%	0.0083
Abiotic: +Year03-04, +Year03-05, + Julian, + Spatial loc, - Elev, - Slope, + Precip	7	-560.77	-558.99	22.06	0.0000	0.0000	24.72%	16.35%	0.0096
Disturbance: +Year03-04, +Year03-05, +Julian, +Spatial location, +People/hr, -Dogs/hr	6	-554.63	-553.32	27.74	0.0000	0.0000	14.24%	6.20%	0.0620
Vegetation canopy: +Year03-04, +Year03-05, + Julian, + Spatial location, - % Cover trees, - Trees12-27, - Trees 28-60, + Trees60, - Snags	9	-554.12	-551.17	29.89	0.0000	0.0000	24.33%	13.17%	0.0358
Vegetation ground: +Year03-04, +Year03-05, + Julian, + Spatial location, - Grasses, + Herbs, + Shrubs, - Bare ground, - Rock, - Litter, - CWD	11	-550.61	-546.14	34.92	0.0000	0.0000	27.32%	13.77%	0.0426
Habitat types 100m: +Year03-04, +Year03-05, + Julian, + Spatial location, + Habitat heterog., +(Habitat $heterog.^2$), +Aspen, + Montane chaparral, + Montane riparian, + Per. grassland, - Red fir/Subalpine conifer, + Sierran mix con/White fir	12	-543.15	-537.77	43.29	0.0000	0.0000	22.84%	6.88%	0.1785
Habitat types 300m: +Year03-04, +Year03-05, + Julian, + Spatial location, + Habitat heterog, - (Habitat $heterog.^2$), + Aspen, - Barren, + Lodegpole pine, - Montane chaparral/Sagebrush, + Montane riparian/Wet meadow, + Per. grassland, - Red fir/Subalpine conifer, + Sierran mixed conifer/White fir	14	-541.37	-533.87	47.19	0.0000	0.0000	27.79%	9.74%	0.1272
Habitat types 500m: [same as 300 m except - Aspen, + Barren, + Montane chaparral/Sagebrush, - Montane riparian/Wet meadow]	14	-538.31	-530.81	50.24	0.0000	0.0000	24.62%	5.78%	0.2330

Appendix 3.10. Model equations for the top ranked reduced models of total relative abundance of terrestrial herbivores for each explanatory factors group. AIC$_{C}$ values that adjust for small sample sizes were used to rank models for comparison. Also presented are the number model parameters (**k**), model likelihood, R^2 and adjusted R^2 (**Adj-R^2**) values and the p-value of the model. A key to the parameter abbreviations is at the bottom of the page.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Development at 300m: 0.008 + 0.006**D300** + 0.007**D300**^{2}	2	-591.95	-591.78	0	1	0.9935	39.71%	37.93%	<0.0001
Development at 100m: 0.008 + 0.010**D100**	1	-581.20	-581.14	10.63	0.0049	0.0049	25.17%	24.08%	<0.0001
Development at 1000m: 0.008 + 0.005**D1000** + 0.007**D1000**^{2}	2	-579.08	-578.90	12.87	0.0016	0.0016	27.72%	25.59%	<0.0001
Predators: 0.008 + 0.005**LOC** + 0.006**CAFA** – 0.005**NSP**	3	-568.69	-568.33	23.44	0.0000	0.0000	19.85%	16.26%	0.0019
Vegetation canopy: 0.007 + 0.006**LOC** + 0.005**CT60**	2	-567.37	-567.20	24.58	0.0000	0.0000	14.76%	12.26%	0.0044
CWHR Habitat types 300m: 0.008 + 0.007**LOC** + 0.005**PGS300** + 0.002**SMC_WFR300**	3	-566.04	-565.68	26.09	0.0000	0.0000	16.97%	13.25%	0.0057
Vegetation ground: 0.007 + 0.005**LOC** + 0.004**HB** – 0.004**RK** – 0.004**LR**	4	-565.66	-565.05	26.72	0.0000	0.0000	19.89%	15.04%	0.005
Abiotic: 0.002 + 0.010**Y3-4** + 0.010**Y3-5** + 0.011**LOC** – 0.007**EL** + 0.007**PRE**	5	-564.96	-564.04	27.74	0.0000	0.0000	22.54%	16.58%	0.0046
Disturbance: 0.008 0.006**LOC** + 0.002**P/H**	2	-563.20	-563.03	28.75	0.0000	0.0000	9.61%	6.95%	0.0322
CWHR Habitat types 500m: 0.005 + 0.005**Y3-4** + 0.0006**LOC** – 0.004**RFR_SCN500** + 0.003**HH500**	4	-562.31	-561.70	30.08	0.0000	0.0000	16.02%	10.93%	0.0198
CWHR Habitat types 100m: 0.003 + 0.008**Y3-4** + 0.008**Y3-5** + 0.005**LOC** + 0.004**ASP100**	4	-561.41	-560.80	30.97	0.0000	0.0000	14.95%	9.79%	0.0284

Key to model parameters **ASP#**: % cover of aspen habitat within '#' meters; **CAFA**: domestic dog presence; **CT60**: count of trees > 60cm dbh; **D#**: % developed within '#' meters; **(D#)^2**: % developed within '#' meters squared; **EL**: elevation; **HB**: % cover of herbs; **HH#**: habitat heterogeneity within '#' meters; **LOC**: spatial location; **LR**: % cover of litter; **NSP**: native predator species richness; **PGS#**: % cover of perennial grassland habitat within '#' meters; **P/H**: people/hr; **PRE**: precipitation; **RK**: % cover of rock; **RFR-SCN#**: % cover of red fir/subalpine conifer habitat within '#' meters; **SMC_WFR#**: % cover of Sierran mixed conifer/white fir habitat within '#' meters; **Y3-4**: year 2004 relative to 2003; **Y3-5**: year 2005 relative to 2003.

Appendix 3.11. Full models of the total relative abundance of insectivores for each explanatory factors group. Individual factors are listed for each group, with the direction of the relationship with insectivore abundance indicated as positive ‘+’ or negative ‘-’ based on the parameter estimates. AIC_C values that adjust for small sample sizes were used to rank models for comparison, and the models are listed from lowest to highest AIC_C. Also presented are the number of model parameters (**k**), model likelihood, model weight (**Wi**), R^2, adjusted R^2 (**Adj-R^2**), and the model p-value.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
Predators: - Spatial location, + Domestic dogs, - Domestic cats, + Native predator species richness	4	-873.59	-872.99	0	1	0.3503	13.21%	7.95%	0.0500
Disturbance: - Spatial location, - People/hr, + Dogs/hr	3	-872.67	-872.31	0.67	0.7148	0.2504	3.63%	-0.69%	0.4761
Development at 100m: - Spatial location, + Development	2	-872.03	-871.85	1.13	0.5678	0.1989	3.14%	0.30%	0.3375
Development at 300m: - Spatial location, + Development, - (Development^2)	3	-870.36	-870.00	2.99	0.2244	0.0786	4.95%	0.70%	0.2874
Development at 1000m: - Spatial location, + Development, - (Development^2)	3	-869.71	-869.35	3.64	0.1623	0.0568	4.22%	-0.07%	0.4061
Abiotic: - Spatial location, + Elevation, - Slope, + Precipitation	4	-869.67	-869.06	3.92	0.1407	0.0493	8.22%	2.66%	0.2191
Vegetation canopy: - Spatial location, - % Cover trees, + Trees12-27, - Trees 28-60, + Trees60, + Snags	6	-866.67	-865.36	7.63	0.0221	0.0077	12.25%	4.03%	0.1961
Habitat types 100m: - Spatial location, - Habitat heterogeneity, - (Habitat heterogeneity^2), +Aspen, + Montane chaparral, + Montane riparian, + Perennial grassland, + Red fir/Subalpine conifer, + Sierran mixed conifer/White fir	9	-868.30	-865.35	7.63	0.0220	0.0077	24.88%	13.79%	0.0307
Vegetation ground: - Spatial location, - Grasses, - Herbs, + Shrubs, + Bare ground, - Rock, + Litter, + CWD	8	-858.59	-856.26	16.72	0.0002	0.0001	9.89%	-1.73%	0.5623
Habitat types 500m: - Spatial location, + Habitat heterogeneity, - (Habitat heterogeneity^2), - Aspen, + Barren, - Lodegpole pine, + Montane chaparral/Sagebrush, - Montane riparian/Wet meadow, + Perennial grassland, + Red fir/Subalpine conifer, + Sierran mixed conifer/White fir	11	-858.72	-854.25	18.74	0.0001	0.0000	21.39%	6.73%	0.1717

Explanatory Factors Group: Model equation	k	AIC	AICc	ΔAICc	Model likelihood	Wi	R^2	Adj - R^2	p-value
Habitat types 300m: - Spatial location, - Habitat heterogeneity, - (Habitat heterogeneity^2), - Aspen, - Barren, - Lodegpole pine, - Montane chaparral/Sagebrush, + Montane riparian/Wet meadow, + Perennial grassland, + Red fir/Subalpine conifer, + Sierran mixed conifer/White fir	11	-857.52	-853.04	19.94	0.0000	0.0000	20.03%	5.12%	0.2244

Appendix 3.12. Model equations for the top ranked reduced models of total relative abundance of insectivores for each explanatory factors group. AIC_C values that adjust for small sample sizes were used to rank models for comparison. Also presented are the number model parameters (**k**), model likelihood, R^2 and adjusted R^2 (**Adj-R^2**) values and the p-value of the model. A key to the parameter abbreviations is at the bottom of the page.

Explanatory Factors Group: Model equation	**k**	**AIC**	**AICc**	**ΔAICc**	**Model likelihood**	**Wi**	**R^2**	**Adj - R^2**	**p-value**
CWHR Habitat types 100m: 0.0009 + 0.0006**MRI100** + 0.0004**RFR_SCN100** + 0.0007**SMC_WFR100**	3	-885.15	-884.79	0	1	0.5115	22.89%	19.44%	0.0005
CWHR Habitat types 500m: 0.0009 + 0.0008**SMC_WFR500**	1	-883.93	-883.87	0.92	0.6318	0.3231	14.59%	13.35%	0.001
CWHR Habitat types 300m: 0.0009 + 0.0007**SMC_WFR300**	1	-882.27	-882.21	2.58	0.2758	0.1411	12.59%	11.32%	0.0024
Predators: 0.0009 + 0.0005**CAFA**	1	-877.18	-877.12	7.67	0.0216	0.0111	6.04%	4.68%	0.0389
Vegetation ground: 0.0009 – 0.0004**LOC** – 0.0004**RK**	2	-875.35	-875.17	9.62	0.0082	0.0042	7.49%	4.77%	0.0707
Vegetation canopy: 0.0009 + 0.0004**CT60**	1	-875.01	-874.95	9.84	0.0073	0.0037	3.12%	1.71%	0.1409
Development at 1000m: 0.0009 – 0.0001**D1000**	1	-873.06	-873.01	11.78	0.0028	0.0014	0.45%	-0.99%	0.578
Development at 300m: 0.0009 – 0.0004**D300**	1	-872.75	-872.69	12.10	0.0024	0.0012	0.04%	-1.41%	0.8639
Abiotic: 0.0009 + 0.0005**EL** – 0.0004**SL**	2	-872.68	-872.51	12.28	0.0022	0.0011	3.98%	1.16%	0.2514
Disturbance: 0.0009 – 0.0004**LOC** – 0.0001**P/H**	2	-872.19	-872.02	12.77	0.0017	0.0009	3.41%	0.57%	0.307
Development at 100m: 0.0009 – 0.0004**LOC** – 0.0003**D100**	2	-872.03	-871.85	12.94	0.0016	0.0008	3.14%	0.30%	0.3375

Key to model parameters **CAFA**: domestic dog presence; **CT60**: count of trees > 60cm dbh; **D#**: % developed within '#' meters; **EL**: elevation; **LOC**: spatial location; **MRI#**: % cover of montane riparian habitat within '#' meters; **P/H**: people/hr; **RK**: % cover of rock; **RFR-SCN#**: % cover of red fir/subalpine conifer habitat within '#' meters; **SMC_WFR#**: % cover of Sierran mixed conifer/white fir habitat within '#' meters.

Appendix 3.13. Population parameter estimates generated by model averaging for the long-eared chipmunk.

	ADULT FEMALES		ADULT MALES		JUVENILE FEMALES		JUVENILE MALES	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Survival (S) 2003-2004	0.4002	0.0348	0.4002	0.0348	0.4001	0.0351	0.4001	0.0352
Survival (S) 2004-2005	0.1415	0.0207	0.1415	0.0207	0.1414	0.0208	0.1414	0.0208
Emigration (Gamma") 2003-2004	0.0070	0.0363	0.1625	0.1043	0.6680	0.2188	0.8400	0.1241
Emigration (Gamma") 2004-2005	0.0070	0.0363	0.1625	0.1043	0.6680	0.2188	0.8400	0.1241
Capture Probability (p) 2003 Occasion 1	0.2098	0.0136	0.1972	0.0148	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2003 Occasion 2	0.2099	0.0136	0.1972	0.0148	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2003 Occasion 3	0.2099	0.0136	0.1972	0.0149	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2003 Occasion 4	0.2099	0.0136	0.1972	0.0148	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2003 Occasion 5	0.2099	0.0136	0.1972	0.0148	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2003 Occasion 6	0.2099	0.0136	0.1972	0.0148	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2003 Occasion 7	0.2099	0.0136	0.1972	0.0148	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2003 Occasion 8	0.2098	0.0136	0.1972	0.0148	0.0620	0.0252	0.1517	0.0328
Capture Probability (p) 2004 Occasion 1	0.4067	0.0122	0.3450	0.0135	0.1966	0.0235	0.1915	0.0264
Capture Probability (p) 2004 Occasion 2	0.4067	0.0122	0.3450	0.0135	0.1966	0.0235	0.1915	0.0264
Capture Probability (p) 2004 Occasion 3	0.4067	0.0122	0.3450	0.0135	0.1966	0.0235	0.1915	0.0264
Capture Probability (p) 2004 Occasion 4	0.4067	0.0122	0.3450	0.0135	0.1966	0.0235	0.1915	0.0264
Capture Probability (p) 2004 Occasion 5	0.4067	0.0122	0.3450	0.0135	0.1966	0.0235	0.1915	0.0264
Capture Probability (p) 2004 Occasion 6	0.4067	0.0122	0.3450	0.0135	0.1966	0.0235	0.1915	0.0264
Capture Probability (p) 2004 Occasion 7	0.4067	0.0122	0.3451	0.0135	0.1966	0.0235	0.1916	0.0264
Capture Probability (p) 2004 Occasion 8	0.4067	0.0122	0.3450	0.0135	0.1966	0.0235	0.1915	0.0264
Capture Probability (p) 2005 Occasion 1	0.1996	0.0197	0.1856	0.0181	0.0733	0.0216	0.1344	0.0256
Capture Probability (p) 2005 Occasion 2	0.1996	0.0197	0.1856	0.0181	0.0733	0.0216	0.1344	0.0255
Capture Probability (p) 2005 Occasion 3	0.1996	0.0197	0.1856	0.0181	0.0733	0.0216	0.1344	0.0255
Capture Probability (p) 2005 Occasion 4	0.1996	0.0197	0.1856	0.0181	0.0733	0.0216	0.1344	0.0255
Capture Probability (p) 2005 Occasion 5	0.1996	0.0197	0.1856	0.0181	0.0733	0.0216	0.1344	0.0255
Capture Probability (p) 2005 Occasion 6	0.1996	0.0197	0.1856	0.0181	0.0733	0.0216	0.1344	0.0255
Capture Probability (p) 2005 Occasion 7	0.1996	0.0197	0.1856	0.0181	0.0733	0.0216	0.1344	0.0255
Capture Probability (p) 2005 Occasion 8	0.1996	0.0197	0.1856	0.0182	0.0733	0.0216	0.1344	0.0256
Population Size (N) 2003	187.0046	7.4167	153.0068	7.3741	57.4130	21.4531	35.2141	5.5609
Population Size (N) 2004	231.0451	1.9942	182.6987	2.7476	60.0089	4.6478	55.8500	4.8320
Population Size (N) 2005	84.8897	5.3911	94.9785	6.2831	69.7588	18.4058	56.6192	8.1239

Appendix 3.14. Population parameter estimates generated by model averaging for the yellow-pine chipmunk.

	ADULT FEMALES		ADULT MALES		JUVENILE FEMALES		JUVENILE MALES	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Survival (S) 2003-2004	0.1661	0.0301	0.1219	0.0237	0.0490	0.0355	0.0335	0.0246
Survival (S) 2004-2005	0.1034	0.0206	0.0746	0.0183	0.0288	0.0207	0.0197	0.0146
Emigration (Gamma") 2003-2004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Emigration (Gamma") 2004-2005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Capture Probability (p) 2003 Occasion 1	0.2041	0.0166	0.1748	0.0149	0.1227	0.0362	0.0589	0.0177
Capture Probability (p) 2003 Occasion 2	0.2074	0.0167	0.1777	0.0150	0.1248	0.0368	0.0600	0.0180
Capture Probability (p) 2003 Occasion 3	0.2718	0.0194	0.2357	0.0178	0.1690	0.0471	0.0834	0.0243
Capture Probability (p) 2003 Occasion 4	0.2361	0.0180	0.2034	0.0163	0.1442	0.0414	0.0701	0.0208
Capture Probability (p) 2003 Occasion 5	0.3095	0.0207	0.2702	0.0193	0.1964	0.0528	0.0986	0.0282
Capture Probability (p) 2003 Occasion 6	0.2476	0.0185	0.2138	0.0168	0.1521	0.0433	0.0743	0.0219
Capture Probability (p) 2003 Occasion 7	0.3104	0.0207	0.2710	0.0193	0.1970	0.0530	0.0989	0.0283
Capture Probability (p) 2003 Occasion 8	0.2559	0.0188	0.2213	0.0172	0.1579	0.0446	0.0774	0.0227
Capture Probability (p) 2004 Occasion 1	0.3797	0.0199	0.2608	0.0176	0.1721	0.0215	0.1344	0.0179
Capture Probability (p) 2004 Occasion 2	0.3844	0.0199	0.2647	0.0177	0.1750	0.0217	0.1367	0.0181
Capture Probability (p) 2004 Occasion 3	0.4712	0.0200	0.3393	0.0194	0.2323	0.0264	0.1843	0.0227
Capture Probability (p) 2004 Occasion 4	0.4246	0.0201	0.2984	0.0186	0.2004	0.0239	0.1576	0.0202
Capture Probability (p) 2004 Occasion 5	0.5170	0.0198	0.3816	0.0201	0.2666	0.0287	0.2135	0.0252
Capture Probability (p) 2004 Occasion 6	0.4401	0.0201	0.3118	0.0189	0.2107	0.0247	0.1662	0.0210
Capture Probability (p) 2004 Occasion 7	0.5180	0.0198	0.3825	0.0202	0.2674	0.0288	0.2141	0.0253
Capture Probability (p) 2004 Occasion 8	0.4509	0.0201	0.3213	0.0191	0.2181	0.0253	0.1724	0.0216
Capture Probability (p) 2005 Occasion 1	0.2582	0.0275	0.1678	0.0193	0.1926	0.0223	0.1486	0.0186
Capture Probability (p) 2005 Occasion 2	0.2620	0.0276	0.1705	0.0195	0.1957	0.0225	0.1511	0.0188
Capture Probability (p) 2005 Occasion 3	0.3361	0.0313	0.2267	0.0236	0.2576	0.0268	0.2025	0.0232
Capture Probability (p) 2005 Occasion 4	0.2954	0.0295	0.1953	0.0214	0.2232	0.0245	0.1737	0.0208
Capture Probability (p) 2005 Occasion 5	0.3782	0.0328	0.2605	0.0258	0.2942	0.0289	0.2337	0.0255
Capture Probability (p) 2005 Occasion 6	0.3087	0.0301	0.2055	0.0221	0.2343	0.0253	0.1829	0.0216
Capture Probability (p) 2005 Occasion 7	0.3791	0.0328	0.2613	0.0258	0.2950	0.0289	0.2344	0.0256
Capture Probability (p) 2005 Occasion 8	0.3182	0.0306	0.2128	0.0227	0.2423	0.0258	0.1896	0.0221
Population Size (N) 2003	156.1700	4.7832	185.8224	6.8489	18.2220	3.6302	70.5906	17.5986
Population Size (N) 2004	196.0804	1.3208	184.6589	3.2236	63.2327	4.0097	86.2958	6.7502
Population Size (N) 2005	44.6066	1.6691	81.2341	4.6875	63.5210	3.4525	85.5782	6.0596

Appendix 3.15. Population parameter estimates generated by model averaging for the shadow chipmunk.

	ADULT FEMALES		**ADULT MALES**		**JUVENILE FEMALES**		**JUVENILE MALES**	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Survival (S) 2003-2004	0.3491	0.0748	0.3484	0.0753	0.3458	0.0842	0.3451	0.0847
Survival (S) 2004-2005	0.1428	0.0556	0.1422	0.0538	0.1388	0.0550	0.1388	0.0550
Capture Probability (p) 2003 Occasion 1	0.1127	0.0475	0.1127	0.0475	0.0398	0.0453	0.0398	0.0453
Capture Probability (p) 2003 Occasion 2	0.1803	0.0577	0.1803	0.0577	0.0669	0.0720	0.0669	0.0720
Capture Probability (p) 2003 Occasion 3	0.5169	0.0748	0.5168	0.0748	0.2586	0.2144	0.2585	0.2144
Capture Probability (p) 2003 Occasion 4	0.2253	0.0627	0.2253	0.0627	0.0866	0.0904	0.0866	0.0904
Capture Probability (p) 2003 Occasion 5	0.3826	0.0729	0.3825	0.0729	0.1680	0.1572	0.1680	0.1572
Capture Probability (p) 2003 Occasion 6	0.3377	0.0709	0.3377	0.0709	0.1425	0.1379	0.1425	0.1379
Capture Probability (p) 2003 Occasion 7	0.2928	0.0683	0.2928	0.0683	0.1189	0.1187	0.1189	0.1187
Capture Probability (p) 2003 Occasion 8	0.2928	0.0683	0.2928	0.0683	0.1189	0.1187	0.1189	0.1187
Capture Probability (p) 2004 Occasion 1	0.1883	0.0564	0.1883	0.0564	0.0812	0.0348	0.0812	0.0348
Capture Probability (p) 2004 Occasion 2	0.2501	0.0623	0.2501	0.0623	0.1127	0.0436	0.1127	0.0436
Capture Probability (p) 2004 Occasion 3	0.1050	0.0444	0.1050	0.0444	0.0428	0.0227	0.0428	0.0227
Capture Probability (p) 2004 Occasion 4	0.4321	0.0705	0.4321	0.0705	0.2248	0.0688	0.2248	0.0688
Capture Probability (p) 2004 Occasion 5	0.5305	0.0705	0.5305	0.0705	0.3009	0.0813	0.3009	0.0813
Capture Probability (p) 2004 Occasion 6	0.5691	0.0697	0.5691	0.0697	0.3348	0.0857	0.3348	0.0857
Capture Probability (p) 2004 Occasion 7	0.5498	0.0702	0.5498	0.0702	0.3176	0.0836	0.3176	0.0836
Capture Probability (p) 2004 Occasion 8	0.6263	0.0676	0.6263	0.0676	0.3896	0.0914	0.3896	0.0914
Capture Probability (p) 2005 Occasion 1	0.0969	0.0650	0.0969	0.0650	0.0266	0.0275	0.0266	0.0275
Capture Probability (p) 2005 Occasion 2	0.3365	0.1032	0.3365	0.1032	0.1145	0.0889	0.1145	0.0889
Capture Probability (p) 2005 Occasion 3	0.3838	0.1060	0.3838	0.1060	0.1371	0.1026	0.1371	0.1026
Capture Probability (p) 2005 Occasion 4	0.2889	0.0992	0.2889	0.0992	0.0939	0.0757	0.0939	0.0757
Capture Probability (p) 2005 Occasion 5	0.3838	0.1060	0.3838	0.1060	0.1371	0.1026	0.1371	0.1026
Capture Probability (p) 2005 Occasion 6	0.6156	0.1046	0.6156	0.1046	0.2900	0.1744	0.2900	0.1744
Capture Probability (p) 2005 Occasion 7	0.4309	0.1077	0.4309	0.1077	0.1618	0.1166	0.1618	0.1166
Capture Probability (p) 2005 Occasion 8	0.6156	0.1046	0.6156	0.1046	0.2900	0.1744	0.2900	0.1744

Appendix 3.16. Population parameter estimates generated by model averaging for the lodgepole chipmunk.

	ADULT FEMALES		**ADULT MALES**		**JUVENILE FEMALES**		**JUVENILE MALES**	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Survival Parameter (S) 2003-2004	0.0498	0.0422	0.0468	0.0397	0.0549	0.0547	0.0520	0.0530
Survival Parameter (S) 2004-2005	0.0498	0.0422	0.0468	0.0397	0.0549	0.0547	0.0520	0.0530
Capture Probability (p) 2003 Occasion 1	0.1133	0.0435	0.1133	0.0435	0.1132	0.0436	0.1132	0.0436
Capture Probability (p) 2003 Occasion 2	0.1888	0.0538	0.1888	0.0538	0.1886	0.0540	0.1886	0.0540
Capture Probability (p) 2003 Occasion 3	0.3020	0.0631	0.3020	0.0631	0.3018	0.0635	0.3018	0.0635
Capture Probability (p) 2003 Occasion 4	0.2642	0.0606	0.2642	0.0606	0.2641	0.0609	0.2641	0.0609
Capture Probability (p) 2003 Occasion 5	0.3209	0.0642	0.3209	0.0642	0.3207	0.0645	0.3207	0.0645
Capture Probability (p) 2003 Occasion 6	0.3775	0.0666	0.3775	0.0666	0.3773	0.0671	0.3773	0.0671
Capture Probability (p) 2003 Occasion 7	0.2831	0.0619	0.2831	0.0619	0.2830	0.0622	0.2830	0.0622
Capture Probability (p) 2003 Occasion 8	0.1888	0.0538	0.1888	0.0538	0.1886	0.0540	0.1886	0.0540
Capture Probability (p) 2004 Occasion 1	0.1133	0.0435	0.1133	0.0435	0.1132	0.0436	0.1132	0.0436
Capture Probability (p) 2004 Occasion 2	0.1888	0.0538	0.1888	0.0538	0.1886	0.0540	0.1886	0.0540
Capture Probability (p) 2004 Occasion 3	0.3020	0.0631	0.3020	0.0631	0.3018	0.0635	0.3018	0.0635
Capture Probability (p) 2004 Occasion 4	0.2642	0.0606	0.2642	0.0606	0.2641	0.0609	0.2641	0.0609
Capture Probability (p) 2004 Occasion 5	0.3209	0.0642	0.3209	0.0642	0.3207	0.0645	0.3207	0.0645
Capture Probability (p) 2004 Occasion 6	0.3775	0.0666	0.3775	0.0666	0.3773	0.0671	0.3773	0.0671
Capture Probability (p) 2004 Occasion 7	0.2831	0.0619	0.2831	0.0619	0.2830	0.0622	0.2830	0.0622
Capture Probability (p) 2004 Occasion 8	0.1888	0.0538	0.1888	0.0538	0.1886	0.0540	0.1886	0.0540
Capture Probability (p) 2005 Occasion 1	0.1133	0.0435	0.1133	0.0435	0.1132	0.0436	0.1132	0.0436
Capture Probability (p) 2005 Occasion 2	0.1888	0.0538	0.1888	0.0538	0.1886	0.0540	0.1886	0.0540
Capture Probability (p) 2005 Occasion 3	0.3020	0.0631	0.3020	0.0631	0.3018	0.0635	0.3018	0.0635
Capture Probability (p) 2005 Occasion 4	0.2642	0.0606	0.2642	0.0606	0.2641	0.0609	0.2641	0.0609
Capture Probability (p) 2005 Occasion 5	0.3209	0.0642	0.3209	0.0642	0.3207	0.0645	0.3207	0.0645
Capture Probability (p) 2005 Occasion 6	0.3775	0.0666	0.3775	0.0666	0.3773	0.0671	0.3773	0.0671
Capture Probability (p) 2005 Occasion 7	0.2831	0.0619	0.2831	0.0619	0.2830	0.0622	0.2830	0.0622
Capture Probability (p) 2005 Occasion 8	0.1888	0.0538	0.1888	0.0538	0.1886	0.0540	0.1886	0.0540

Appendix 3.17. Population parameter estimates generated by model averaging for the California ground squirrel.

	ADULT FEMALES		**ADULT MALES**		**JUVENILE FEMALES**		**JUVENILE MALES**	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Survival Parameter (S) 2003-2004	0.4486	0.1333	0.1274	0.0622	0.4485	0.1334	0.1274	0.0621
Survival Parameter (S) 2004-2005	0.4486	0.1333	0.1275	0.0623	0.4486	0.1334	0.1274	0.0623
Emigration (Gamma") 2003-2004	0.4000	0.1836	0.4000	0.1836	0.9410	0.0472	0.9410	0.0472
Emigration (Gamma") 2004-2005	0.4000	0.1836	0.4000	0.1836	0.9410	0.0472	0.9410	0.0472
Capture Probability (p) 2003 Occasion 1	0.0970	0.0166	0.0825	0.0150	0.0772	0.0148	0.0786	0.0154
Capture Probability (p) 2003 Occasion 2	0.0873	0.0154	0.0741	0.0139	0.0694	0.0137	0.0706	0.0142
Capture Probability (p) 2003 Occasion 3	0.1712	0.0244	0.1474	0.0228	0.1386	0.0230	0.1409	0.0238
Capture Probability (p) 2003 Occasion 4	0.1402	0.0213	0.1201	0.0197	0.1127	0.0197	0.1146	0.0204
Capture Probability (p) 2003 Occasion 5	0.2414	0.0304	0.2104	0.0291	0.1987	0.0297	0.2017	0.0308
Capture Probability (p) 2003 Occasion 6	0.1677	0.0240	0.1443	0.0224	0.1357	0.0226	0.1379	0.0234
Capture Probability (p) 2003 Occasion 7	0.2489	0.0309	0.2172	0.0297	0.2052	0.0304	0.2083	0.0315
Capture Probability (p) 2003 Occasion 8	0.1504	0.0224	0.1291	0.0207	0.1212	0.0208	0.1233	0.0216
Capture Probability (p) 2004 Occasion 1	0.2043	0.0270	0.1769	0.0256	0.1667	0.0245	0.1693	0.0250
Capture Probability (p) 2004 Occasion 2	0.1860	0.0259	0.1606	0.0243	0.1512	0.0232	0.1536	0.0237
Capture Probability (p) 2004 Occasion 3	0.3304	0.0327	0.2924	0.0327	0.2777	0.0318	0.2815	0.0324
Capture Probability (p) 2004 Occasion 4	0.2803	0.0309	0.2459	0.0302	0.2328	0.0292	0.2363	0.0298
Capture Probability (p) 2004 Occasion 5	0.4320	0.0348	0.3890	0.0362	0.3721	0.0356	0.3765	0.0362
Capture Probability (p) 2004 Occasion 6	0.3249	0.0325	0.2873	0.0325	0.2728	0.0315	0.2766	0.0321
Capture Probability (p) 2004 Occasion 7	0.4419	0.0349	0.3986	0.0364	0.3815	0.0359	0.3860	0.0365
Capture Probability (p) 2004 Occasion 8	0.2973	0.0315	0.2615	0.0311	0.2479	0.0301	0.2515	0.0307
Capture Probability (p) 2005 Occasion 1	0.1492	0.0214	0.1280	0.0205	0.1202	0.0190	0.1222	0.0196
Capture Probability (p) 2005 Occasion 2	0.1351	0.0203	0.1156	0.0192	0.1085	0.0178	0.1103	0.0184
Capture Probability (p) 2005 Occasion 3	0.2521	0.0283	0.2201	0.0285	0.2080	0.0267	0.2112	0.0275
Capture Probability (p) 2005 Occasion 4	0.2102	0.0258	0.1822	0.0255	0.1717	0.0238	0.1745	0.0246
Capture Probability (p) 2005 Occasion 5	0.3419	0.0323	0.3031	0.0339	0.2882	0.0320	0.2921	0.0329
Capture Probability (p) 2005 Occasion 6	0.2475	0.0280	0.2159	0.0282	0.2040	0.0264	0.2071	0.0272
Capture Probability (p) 2005 Occasion 7	0.3510	0.0326	0.3117	0.0343	0.2965	0.0324	0.3005	0.0334
Capture Probability (p) 2005 Occasion 8	0.2242	0.0267	0.1948	0.0266	0.1838	0.0248	0.1867	0.0256
Population Size (N) 2003	54.5179	5.1409	50.4560	5.8129	25.8682	4.0911	18.3625	3.3022
Population Size (N) 2004	41.4485	1.5466	36.0933	1.8409	37.6647	2.0634	37.5276	2.0182
Population Size (N) 2005	49.9619	2.7892	32.3905	2.7114	48.7384	3.7074	42.4737	3.3674

Appendix 3.18. Population parameter estimates generated by model averaging for the golden-mantled ground squirrel.

	ADULT FEMALES		**ADULT MALES**		**JUVENILE FEMALES**		**JUVENILE MALES**	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Survival Parameter (S) 2003-2004	0.4199	0.1632	0.4199	0.1632	0.0354	0.0386	0.0354	0.0386
Survival Parameter (S) 2004-2005	0.4199	0.1632	0.4199	0.1632	0.0354	0.0386	0.0354	0.0386
Emigration (Gamma") 2003-2004	0.4364	0.2309	0.4364	0.2309	0.4364	0.2309	0.4364	0.2309
Emigration (Gamma") 2004-2005	0.5396	0.2549	0.5396	0.2549	0.5396	0.2549	0.5396	0.2549
Capture Probability (p) 2003 Occasion 1	0.2185	0.0292	0.2740	0.0346	0.1503	0.0264	0.1370	0.0239
Capture Probability (p) 2003 Occasion 2	0.1799	0.0272	0.2286	0.0332	0.1220	0.0235	0.1109	0.0211
Capture Probability (p) 2003 Occasion 3	0.3434	0.0347	0.4138	0.0387	0.2486	0.0361	0.2290	0.0330
Capture Probability (p) 2003 Occasion 4	0.1880	0.0272	0.2382	0.0327	0.1278	0.0237	0.1162	0.0214
Capture Probability (p) 2003 Occasion 5	0.2908	0.0328	0.3563	0.0372	0.2060	0.0320	0.1889	0.0293
Capture Probability (p) 2003 Occasion 6	0.2564	0.0314	0.3176	0.0367	0.1791	0.0298	0.1638	0.0270
Capture Probability (p) 2003 Occasion 7	0.4070	0.0363	0.4809	0.0388	0.3027	0.0399	0.2804	0.0370
Capture Probability (p) 2003 Occasion 8	0.1847	0.0277	0.2342	0.0326	0.1253	0.0232	0.1140	0.0213
Capture Probability (p) 2004 Occasion 1	0.2184	0.0291	0.2742	0.0343	0.1506	0.0260	0.1372	0.0236
Capture Probability (p) 2004 Occasion 2	0.1809	0.0272	0.2298	0.0326	0.1229	0.0232	0.1117	0.0212
Capture Probability (p) 2004 Occasion 3	0.3435	0.0346	0.4143	0.0380	0.2493	0.0353	0.2295	0.0326
Capture Probability (p) 2004 Occasion 4	0.1885	0.0276	0.2389	0.0329	0.1284	0.0237	0.1168	0.0217
Capture Probability (p) 2004 Occasion 5	0.2911	0.0328	0.3569	0.0370	0.2067	0.0317	0.1894	0.0292
Capture Probability (p) 2004 Occasion 6	0.2572	0.0318	0.3189	0.0365	0.1802	0.0296	0.1647	0.0273
Capture Probability (p) 2004 Occasion 7	0.4072	0.0363	0.4814	0.0386	0.3035	0.0394	0.2810	0.0368
Capture Probability (p) 2004 Occasion 8	0.1845	0.0270	0.2342	0.0324	0.1255	0.0232	0.1141	0.0211
Capture Probability (p) 2005 Occasion 1	0.2191	0.0299	0.2754	0.0363	0.1514	0.0274	0.1375	0.0239
Capture Probability (p) 2005 Occasion 2	0.1802	0.0268	0.2294	0.0322	0.1225	0.0229	0.1111	0.0207
Capture Probability (p) 2005 Occasion 3	0.3437	0.0349	0.4149	0.0390	0.2497	0.0360	0.2293	0.0326
Capture Probability (p) 2005 Occasion 4	0.1875	0.0280	0.2380	0.0331	0.1278	0.0237	0.1160	0.0217
Capture Probability (p) 2005 Occasion 5	0.2904	0.0331	0.3565	0.0372	0.2063	0.0318	0.1887	0.0293
Capture Probability (p) 2005 Occasion 6	0.2561	0.0319	0.3179	0.0363	0.1795	0.0293	0.1637	0.0270
Capture Probability (p) 2005 Occasion 7	0.4065	0.0368	0.4811	0.0388	0.3031	0.0394	0.2801	0.0370
Capture Probability (p) 2005 Occasion 8	0.1834	0.0286	0.2330	0.0340	0.1248	0.0238	0.1133	0.0218
Population Size (N) 2003	34.1171	0.6871	21.0866	0.6366	16.7766	1.3744	10.7462	1.4085
Population Size (N) 2004	32.1171	0.6871	35.0866	0.6366	27.7766	1.3744	29.7462	1.4085
Population Size (N) 2005	18.1171	0.6871	17.0866	0.6366	16.7766	1.3744	26.7462	1.4085

Appendix 3.19. Population parameter estimates generated by model averaging for the Douglas squirrel.

	ADULT FEMALES		**ADULT MALES**		**JUVENILE FEMALES**		**JUVENILE MALES**	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Survival Parameter (S) 2003-2004	0.0960	0.0315	0.0940	0.0323	0.0960	0.0315	0.0940	0.0323
Survival Parameter (S) 2004-2005	0.0898	0.0300	0.0898	0.0300	0.0878	0.0304	0.0878	0.0304
Capture Probability (p) 2003 Occasion 1	0.1176	0.0184	0.1176	0.0184	0.1176	0.0184	0.1176	0.0184
Capture Probability (p) 2003 Occasion 2	0.2100	0.0248	0.2100	0.0248	0.2100	0.0248	0.2100	0.0248
Capture Probability (p) 2003 Occasion 3	0.0896	0.0160	0.0896	0.0160	0.0896	0.0160	0.0896	0.0160
Capture Probability (p) 2003 Occasion 4	0.1736	0.0225	0.1736	0.0225	0.1736	0.0225	0.1736	0.0225
Capture Probability (p) 2003 Occasion 5	0.1008	0.0170	0.1008	0.0170	0.1008	0.0170	0.1008	0.0170
Capture Probability (p) 2003 Occasion 6	0.1708	0.0223	0.1708	0.0223	0.1708	0.0223	0.1708	0.0223
Capture Probability (p) 2003 Occasion 7	0.0812	0.0152	0.0812	0.0152	0.0812	0.0152	0.0812	0.0152
Capture Probability (p) 2003 Occasion 8	0.0924	0.0162	0.0924	0.0162	0.0924	0.0162	0.0924	0.0162
Capture Probability (p) 2004 Occasion 1	0.1176	0.0184	0.1176	0.0184	0.1176	0.0184	0.1176	0.0184
Capture Probability (p) 2004 Occasion 2	0.2100	0.0248	0.2100	0.0248	0.2100	0.0248	0.2100	0.0248
Capture Probability (p) 2004 Occasion 3	0.0896	0.0160	0.0896	0.0160	0.0896	0.0160	0.0896	0.0160
Capture Probability (p) 2004 Occasion 4	0.1736	0.0225	0.1736	0.0225	0.1736	0.0225	0.1736	0.0225
Capture Probability (p) 2004 Occasion 5	0.1008	0.0170	0.1008	0.0170	0.1008	0.0170	0.1008	0.0170
Capture Probability (p) 2004 Occasion 6	0.1708	0.0223	0.1708	0.0223	0.1708	0.0223	0.1708	0.0223
Capture Probability (p) 2004 Occasion 7	0.0812	0.0152	0.0812	0.0152	0.0812	0.0152	0.0812	0.0152
Capture Probability (p) 2004 Occasion 8	0.0924	0.0162	0.0924	0.0162	0.0924	0.0162	0.0924	0.0162
Capture Probability (p) 2005 Occasion 1	0.1176	0.0184	0.1176	0.0184	0.1176	0.0184	0.1176	0.0184
Capture Probability (p) 2005 Occasion 2	0.2100	0.0248	0.2100	0.0248	0.2100	0.0248	0.2100	0.0248
Capture Probability (p) 2005 Occasion 3	0.0896	0.0160	0.0896	0.0160	0.0896	0.0160	0.0896	0.0160
Capture Probability (p) 2005 Occasion 4	0.1736	0.0225	0.1736	0.0225	0.1736	0.0225	0.1736	0.0225
Capture Probability (p) 2005 Occasion 5	0.1008	0.0170	0.1008	0.0170	0.1008	0.0170	0.1008	0.0170
Capture Probability (p) 2005 Occasion 6	0.1708	0.0223	0.1708	0.0223	0.1708	0.0223	0.1708	0.0223
Capture Probability (p) 2005 Occasion 7	0.0812	0.0152	0.0812	0.0152	0.0812	0.0152	0.0812	0.0152
Capture Probability (p) 2005 Occasion 8	0.0924	0.0162	0.0924	0.0162	0.0924	0.0162	0.0924	0.0162
Population Size (N) 2003	42.5304	4.9498	48.4667	5.3342	23.2360	3.5521	14.3285	2.7684
Population Size (N) 2004	48.4666	5.3342	61.8230	6.1531	6.8973	1.9308	15.8136	2.9118
Population Size (N) 2005	27.6889	3.9023	44.0145	5.0474	8.3849	2.1190	15.8136	2.9118

Appendix 5.1 - Ants recorded in pitfall traps at 103 sites sampled along an development gradient in the Lake Tahoe Basin 2003 to 2004.

Ant Taxa	Mean Body Length (mm)	Nesting Strategies	Nest Types	Continental Grouping
Myrmicinae				
Aphaenogaster occidentalis	3.92	3	stones, logs, ground	Opportunist
Leptothorax calderona	3.09	1	logs	Cold Climate Specialist
Leptothorax muscorum	3.1	1	logs	Cold Climate Specialist
Manica bradleyi	5.14	1	ground	Cold Climate Specialist
Manica invadia	4.75	1	ground	Cold Climate Specialist
Myrmica discontinua	3	1	stones	Opportunist
Myrmica tahoensis	4	1	stones	Opportunist
Stenamma smithi	UNDET	1	ground	Cold Climate Specialist
Temnothorax cf. rugatulus	2.6	1	arboreal	Cold Climate Specialist
Temnothorax nitens	2.2	1	stones	Cold Climate Specialist
Temnothorax nevadensis	2.5	2	stones, ground	Cold Climate Specialist
Temnothorax rugatulus	2.66	1	stones	Cold Climate Specialist
Tetrramorium caespitum	2.96	2	stones, ground	Opportunist
Dolichoderinae				
Dolichoderine sp. 1	UNDET	UNDET	UNDET	UNDET
Liometopum occidentale	3.86	1	arboreal	Dominant Dolichoderinae
Tapinoma sessile	2.44	3	stones, logs, ground	Opportunist
Formicinae				
Camponotus essigi	6	1	arboreal	Subordinate Camponotini
Camponotus hyatti	4.73	1	ground	Subordinate Camponotini
Camponotus laevigatus	9.5	1	logs	Subordinate Camponotini
Camponotus modoc	8	1	logs	Subordinate Camponotini
Camponotus vicinus	10.9	3	stones, logs, ground	Subordinate Camponotini
Formica sp. 1	UNDET	UNDET	UNDET	Cold Climate Specialist
Formica accreta	5.4	1	logs	Opportunists
Formica argentea	5.4	2	stones, ground	Opportunists
Formica aserva	7.27	1	logs	Cold Climate Specialist
Formica CA-01	5.8	2	stones, ground (some thatch)	Cold Climate Specialist
Formica cf. sybilla	5.6	1	ground	Opportunists
Formica dakotensis	4.75	2	stones, ground (some thatch)	Cold Climate Specialist
Formica fusca	3.95	2	stones, ground	Opportunists
Formica integroides	6.63	1	mound nest w/ thatch	Cold Climate Specialist
Formica lasiodes	4.25	2	stones, ground	Opportunists
Formica microphthalma	4.66	2	stones, ground	Opportunists
Formica neoclara	3.84	1	ground	Opportunists
Formica neogagates	4.43	2	stones, ground	Opportunists
Formica neorufibarbus	4.8	3	stones, logs, ground	Opportunists
Formica nevadensis	4.95	1	stones, ground (some thatch)	Cold Climate Specialist
Formica obscruipes	6.64	1	mound nest w/ thatch	Cold Climate Specialist
Formica propinqua	7	1	mound nest w/ thatch	Cold Climate Specialist
Formica ravida	5.68	1	mound nest w/ thatch	Cold Climate Specialist
Formica rufa group sp 1	UNDET	UNDET	UNDET	Cold Climate Specialist
Formica sibylla	5	1	ground	Opportunists
Formica subpolita	5.48	2	stones, ground	Cold Climate Specialist
Lasius flavus	2.7	2	stones, ground	Cold Climate Specialist
Lasius pallitarsis	3.73	3	stones, logs, ground	Cold Climate Specialist
Myrmecocystus sp. 2	UNDET	1	ground	Hot Climate Specialists
Myrmecocystus testaceus	4.94	1	ground	Hot Climate Specialists

Appendix 5.2 - Univariate responses of individual ant species abundance in the Lake Tahoe basin to multiple scales of urban development. Scales of development were calculated within 60, 100, 500, and 1000 m of the center of each sample site. Responses indicate the direction of the slope for univariate regressions. Species with no data were too rare for analysis.

	60-m Scale			*100-m Scale*			*300-m Scale*			*500-m Scale*			*1000-m Scale*		
Ant Species	*Response*	*Adj R^2*	*P*	*Response*	*Adj R^2*	*P*	*Response*	*Adj R^2*	*P*	*Response*	*Adj R^2*	*P*	*Response*	*Adj R^2*	*P*
Aphaenogaster occidentalis	–	0.0724	0.8017	+	0.0452	0.9372	+	0.0271	0.5369	+	0.0081	0.2876	+	0.0271	0.2135
Camponotus essigi	–	0.114	0.5616	–	0.1136	0.5606	–	0.001	0.3619	–	0.0372	0.3175	–	0.0701	0.2821
Camponotus hyatti															
Camponotus laevigatus	–	0.0289	0.222	–	0.0763	0.1199	–	0.1585	0.0418	–	0.195	0.3246	–	0.0357	0.2027
Camponotus modoc	–	0.0213	0.1137	–	0.0219	0.1091	–	0.0187	0.1263	–	0.0176	0.1334	–	0.0178	0.1319
Camponotus vicinus	**–**	**0.1057**	**0.0098**	**–**	**0.0438**	**0.0679**	**–**	**0.0226**	**0.0982**	**–**	**0.007**	**0.2169**	**–**	**0.0011**	**0.2999**
Dolichoderine sp. 1															
Formica accreta	**–**	**0.0493**	**0.0382**	**–**	**0.021**	**0.1235**	**–**	**0.0007**	**0.3325**	**–**	**0.0038**	**0.3904**	**–**	**0.003**	**0.3754**
Formica argentea	+	0.0014	0.3101	+	0.015	0.5331	–	0.0245	0.8873	–	0.0237	0.8196	–	0.0143	0.5188
Formica aserva	–	0.0398	0.6954	–	0.0387	0.7088	+	0.0455	0.9937	–	0.0446	0.895	–	0.0422	0.7969
Formica CA-01															
Formica cf. sibylla	**–**	**0.0912**	**0.0064**	**–**	**0.0911**	**0.0061**	**–**	**0.067**	**0.016**	**–**	**0.0353**	**0.1082**	**–**	**0.058**	**0.0234**
Formica fusca	+	0.0245	0.8843	+	0.0243	0.9491	+	0.0239	0.8901	+	0.0242	0.9288	+	0.0225	0.783
Formica integroides	–	0.1671	0.7226	–	0.1682	0.7275	–	0.0891	0.5075	–	0.0772	0.4844	–	0.0332	0.3221
Formica lasioides	–	0.0208	0.9745	+	0.019	0.7676	+	0.011	0.4975	+	0.0197	0.8185	+	0.0159	0.633
Formica microphthalma	–	0.0419	0.5815	–	0.0421	0.5833	+	0.0557	0.7527	+	0.0594	0.8319	+	0.0587	0.8136
Formica neoclara	**–**	**0.0246**	**0.4612**	**+**	**0.1708**	**0.1158**	**+**	**0.0878**	**0.1099**	**+**	**0.1358**	**0.0613**	**+**	**0.2178**	**0.0219**
Formica neogagates															
Formica neorufibarbus	–	0.0074	0.2929	–	0.0094	0.385	–	0.0317	0.5933	–	0.025	0.5145	–	0.0415	0.7763
Formica obscuripes	+	0.1094	0.5981	+	0.1093	0.5977	+	0.3173	0.166	+	0.049	0.4433	+	0.1577	0.8368
Formica propinqua	–	0.2036	0.7145	–	0.1669	0.6219	–	0.1809	0.6537	–	0.2489	0.9547	–	0.2497	0.9771
Formica ravida	**+**	**0.6686**	**0.0215**	**+**	**0.719**	**0.0133**	**+**	**0.5439**	**0.0141**	**+**	**0.0448**	**0.2673**	**+**	**0.0502**	**0.259**
Formica rufa group sp 1	–	0.0072	0.3842	–	0.0225	0.5192	–	0.0122	0.2614	–	0.0305	0.1897	–	0.0342	0.178
Formica sibylla	**+**	**0.0497**	**0.0525**	**+**	**0.0212**	**0.1423**	**+**	**0.0088**	**0.4783**	**+**	**0.0153**	**0.694**	**+**	**0.0073**	**0.4445**
Formica subpolita	–	0.1108	0.6025	–	0.1227	0.6451	–	0.1666	0.9914	–	0.1586	0.8452	–	0.0864	0.5304
Lasius flavus															
Lasius pallitarsis	–	0.0238	0.6872	–	0.0195	0.5923	+	0.0167	0.5357	+	0.0017	0.309	+	0.0214	0.1869
Leptothorax calderona															
Leptothorax muscorum															
Liometopum occidentale															
Manica bradleyi	+	0.0964	0.2344	+	0.0413	0.2974	+	0.0969	0.5593	+	0.0538	0.2818	+	0.1093	0.2217
Manica invidia	+	0.4655	0.6541	–	0.9421	0.8912	–	0.8595	0.1708	–	0.8793	0.158	–	0.8462	0.8211
Myrmecocystus sp. 2															
Myrmecocystus testaceus															
Myrmica discontinua	–	0.3288	0.9254	–	0.3254	0.9021	+	0.1684	0.5616	+	0.0454	0.3551	–	0.3211	0.8784
Myrmica tahoensis	+	0.0139	0.7791	+	0.0147	0.9007	+	0.0145	0.8609	+	0.0144	0.8485	+	0.0148	0.9202
Tapinoma sessile	–	0.008	0.203	–	0.0023	0.3685	–	0.0055	0.4559	–	0.0046	0.4289	–	0.0063	0.4826
Temnothorax cf. rugatulus	+	0.3628	0.6976	–	0.4646	0.8464	–	0.1829	0.3253	–	0.0326	0.2579	–	0.019	0.4337
Temnothorax nevadensis	–	0.0307	0.1241	–	0.0196	0.1726	–	0.0168	0.6277	–	0.0176	0.653	–	0.0219	0.9098
Temnothorax nitens	**–**	**0.3019**	**0.0086**	**+**	**0.0121**	**0.4215**	**+**	**0.0066**	**0.3746**	**+**	**0.0003**	**0.3241**	**+**	**0.0407**	**0.1506**
Temnothorax rugatulus	–	0.0614	0.3324	+	0.0686	0.5643	+	0.0879	0.6713	+	0.0934	0.7115	+	0.0863	0.6613
Tetramorium caespitum															

Appendix 8.1 – Table of GIS predictive model coefficients for various biodiversity measures. [grayed lettering indicates incomplete information]. Take the antilog of the sum of these values to derive predicted value.

Reponse variable	Predictor variable	Coefficient	Standardized	Mean	s.d.
BIRDS					
Bird species richness					
	Intercept	2.761917E+00			
	dev150	-5.233476E-03	Y	2.619E+01	2.326E+01
	dev300	-1.307186E-02	Y	2.665E+01	2.109E+01
	dev500	-4.471925E-02	Y	2.680E+01	1.948E+01
	dev1000	-2.996104E-02	Y	2.444E+01	1.577E+01
	as150	-3.111376E-03	Y	7.386E-03	3.497E-02
	as300	2.576417E-02	Y	8.079E-03	2.532E-02
	hc300	-7.145868E-15	Y	4.376E-02	9.475E-02
	hc1000	3.709246E-02	Y	6.456E-02	9.098E-02
	hc10002	1.578597E-02	Y	1.242E-02	3.139E-02
	lc150	5.405713E-03	Y	8.102E-01	2.345E-01
	lc300	3.612169E-02	Y	7.958E-01	1.978E-01
	lc500	2.030180E-03	Y	7.726E-01	1.739E-01
	lc1000	-1.315528E-03	Y	7.127E-01	1.540E-01
	rm300rt	6.155648E-04	Y	7.895E-02	1.459E-01
	rm1000rt	1.063730E-02	Y	1.472E-01	1.155E-01
	sh500	-5.815063E-05	Y	2.954E-02	3.646E-02
	CC100	6.029302E-03	Y	3.726E+01	1.340E+01
	ndvi	9.005281E-02	Y	4.512E-01	9.681E-02
	bright	-6.247615E-02	Y	-7.412E-02	2.924E-02
	elev	-4.729651E-01	Y	1.972E+03	5.950E+01
	elev2	3.921218E-01	Y	3.891E+06	2.378E+05
	Slope	7.313019E-02	Y	7.459E+00	5.486E+00
	Slope2	-8.764273E-02	Y	8.565E+01	1.131E+02
	DistWtr	4.291324E-02	Y	4.422E+02	3.515E+02
	DistWtr2	-1.373658E-02	Y	3.188E+05	5.197E+05
	UTM_N	4.410648E+01	Y	4.326E+06	1.625E+04
	UTM_N2	-4.409725E+01	Y	1.871E+13	1.406E+11
	UTM_E	-1.055225E-39	Y	7.585E+05	6.293E+03
Bird community dominance					
	Intercept	-1.519717E+00	Y		
	dev150	5.468916E-04	Y	2.619E+01	2.326E+01
	dev300	2.197335E-02	Y	2.665E+01	2.109E+01
	dev500	9.101791E-02	Y	2.680E+01	1.948E+01
	dev1000	1.644776E-04	Y	2.444E+01	1.577E+01
	as1000	-1.612093E-02	Y	1.214E-02	3.065E-02
	hc150	-5.136887E-07	Y	4.401E-02	1.351E-01
	hc300	-2.053060E-05	Y	4.376E-02	9.475E-02
	hc500	-3.802452E-15	Y	4.652E-02	7.989E-02
	hc1000	2.672605E-15	Y	6.456E-02	9.098E-02

lc150	-2.060517E-04	Y	8.102E-01	2.345E-01
lc300	-5.261541E-03	Y	7.958E-01	1.978E-01
lc500	-4.551952E-03	Y	7.726E-01	1.739E-01
lc1000	1.960062E-13	Y	7.127E-01	1.540E-01
rm150rt	-6.365310E-09	Y	5.484E-02	1.412E-01
rm300rt	-1.383112E-06	Y	7.895E-02	1.459E-01
rm500rt	5.999844E-11	Y	1.012E-01	1.400E-01
rm1000rt	1.821524E-19	Y	1.472E-01	1.155E-01
sh150rt	-5.062754E-05	Y	8.404E-02	1.369E-01
sh300	-5.999151E-09	Y	2.711E-02	4.134E-02
sh1000rt	-7.594425E-18	Y	1.526E-01	8.610E-02
CC100	-1.484841E-06	Y	3.726E+01	1.340E+01
ndvi	-1.475162E-01	Y	4.512E-01	9.681E-02
bright	-2.540064E-10	Y	-7.412E-02	2.924E-02
elev	1.208654E-02	Y	1.972E+03	5.950E+01
Slope	4.265864E-03	Y	7.459E+00	5.486E+00
DistWtr	-6.586596E-02	Y	4.422E+02	3.515E+02
UTM_N	-1.074267E-12	Y	4.326E+06	1.625E+04
UTM_E	3.088336E-17	Y	7.585E+05	6.293E+03

Ground-nesting bird richness

Intercept	6.698941E-01	Y		
dev150	-4.604346E-04	Y	2.619E+01	2.326E+01
dev300	-4.100755E-05	Y	2.665E+01	2.109E+01
dev500	-1.360290E-06	Y	2.680E+01	1.948E+01
dev1000	-2.457877E-01	Y	2.444E+01	1.577E+01
as150	9.099536E-02	Y	7.386E-03	3.497E-02
as300	3.162181E-03	Y	8.079E-03	2.532E-02
as500rt	4.849039E-03	Y	4.503E-02	8.429E-02
as1000	-9.348378E-02	Y	1.214E-02	3.065E-02
hc150	-5.181354E-05	Y	4.401E-02	1.351E-01
hc300	1.022177E-02	Y	4.376E-02	9.475E-02
hc500	8.792540E-02	Y	4.652E-02	7.989E-02
hc1000	1.016027E-02	Y	6.456E-02	9.098E-02
lc150	6.071216E-03	Y	8.102E-01	2.345E-01
lc300	2.447401E-01	Y	7.958E-01	1.978E-01
lc500	9.950144E-05	Y	7.726E-01	1.739E-01
lc1000	1.366917E-05	Y	7.127E-01	1.540E-01
rm150rt	1.341687E-01	Y	5.484E-02	1.412E-01
rm1000rt	5.695662E-03	Y	1.472E-01	1.155E-01
sh150rt	3.908762E-03	Y	8.404E-02	1.369E-01
sh1000rt	3.213186E-02	Y	1.526E-01	8.610E-02
CC100	-2.481357E-03	Y	3.726E+01	1.340E+01
ndvi	1.801317E-02	Y	4.512E-01	9.681E-02
bright	-1.807533E-03	Y	-7.412E-02	2.924E-02
elev	2.581573E+00	Y	1.972E+03	5.950E+01
elev2	-2.571908E+00	Y	3.891E+06	2.378E+05
Slope	1.110673E-01	Y	7.459E+00	5.486E+00
slope2	3.276833E-03	Y	8.565E+01	1.131E+02
DistWtr	2.772098E-02	Y	4.422E+02	3.515E+02

distwtr2	-1.641844E-02	Y	3.188E+05	5.197E+05
UTM_N	1.734806E-04	Y	4.326E+06	1.625E+04
UTM_E	-5.898716E-02	Y	7.585E+05	6.293E+03

Cavity-nesting bird richness

Intercept	1.551875E+00	Y		
dev150	-6.311928E-03	Y	2.619E+01	2.326E+01
dev300	-4.985314E-02	Y	2.665E+01	2.109E+01
dev500	-2.197793E-02	Y	2.680E+01	1.948E+01
dev1000	-1.509933E-04	Y	2.444E+01	1.577E+01
as150	-6.857170E-03	Y	7.386E-03	3.497E-02
as300	9.823199E-03	Y	8.079E-03	2.532E-02
as500rt	-8.956940E-04	Y	4.503E-02	8.429E-02
as1000	-4.626625E-03	Y	1.214E-02	3.065E-02
hc150	-3.001697E-04	Y	4.401E-02	1.351E-01
hc300	-8.683471E-03	Y	4.376E-02	9.475E-02
hc500	5.758848E-05	Y	4.652E-02	7.989E-02
hc1000	2.961482E-04	Y	6.456E-02	9.098E-02
lc150	5.505186E-03	Y	8.102E-01	2.345E-01
lc300	2.840666E-04	Y	7.958E-01	1.978E-01
lc500	-4.125220E-04	Y	7.726E-01	1.739E-01
lc1000	-2.913288E-03	Y	7.127E-01	1.540E-01
rm150rt	3.838475E-03	Y	5.484E-02	1.412E-01
rm300rt	9.351961E-04	Y	7.895E-02	1.459E-01
rm500rt	-7.696877E-06	Y	1.012E-01	1.400E-01
rm1000rt	3.622334E-04	Y	1.472E-01	1.155E-01
sh300	-2.904254E-03	Y	2.711E-02	4.134E-02
sh500	-3.143030E-02	Y	2.954E-02	3.646E-02
sh1000rt	-5.246323E-04	Y	1.526E-01	8.610E-02
CC100	5.640829E-01	Y	3.726E+01	1.340E+01
CC1002	-4.477797E-01	Y	1.567E+03	1.004E+03
ndvi	3.414135E-02	Y	4.512E-01	9.681E-02
bright	-1.107813E-01	Y	-7.412E-02	2.924E-02
elev	-3.493802E-04	Y	1.972E+03	5.950E+01
Slope	-6.007440E-03	Y	7.459E+00	5.486E+00
DistWtr	4.813085E-02	Y	4.422E+02	3.515E+02
UTM_N	2.214199E-03	Y	4.326E+06	1.625E+04
UTM_E	-9.148561E-06	Y	7.585E+05	6.293E+03

LARGE MAMMALS

Marten presence

Intercept	-9.468030E+00	
BAR_300	-3.000000E-05	N
BRI_3X3	2.893075E+01	N
DEV_1000M	-8.780000E-03	N
DEV_300M	-1.525000E-02	N
DEV_500M	-1.065300E-01	N

DIST_STRM	1.250000E-03	N
ELEV	1.170000E-03	N
FOR_1K	6.500000E-04	N
FOR_300	-1.873000E-02	N
GRE_3X3	9.300000E-04	N
MDW_1K	2.647300E-01	N
MDW_300	1.615800E-01	N
N34MD_1K	4.000000E-05	N

Coyote presence

Intercept	1.336330E+00	
DEV_1000M	2.971000E-02	N
DEV_100M	-7.790000E-03	N
DEV_300M	-1.320000E-03	N
DEV_500M	1.580000E-03	N
DEV_MAX	-4.100000E-03	N
DIST_STRM	-3.530000E-03	N
ELEV	-2.000000E-05	N
FOR_1K	-7.000000E-05	N
FOR_300	-6.900000E-04	N
GRE_3X3	-9.460500E+00	N
MDW_1K	2.837830E+00	N
N34MD_300	1.300000E-04	N
N34SP_1K	-2.100000E-04	N
N34SP_300	-7.560000E-03	N
N56MD_1K	-2.060100E-01	N
N56MD_300	-2.950000E-03	N
N56SP_1K	2.481000E-02	N
NDVI_3X3	-1.457180E+00	N
PPT_MM	-1.100000E-04	N
SHR_1K	5.151100E-01	N
SHR_300	4.650000E-03	N
SLOPE_3X3	3.396000E-02	N

Black bear presence

SMALL MAMMALS

Small mammal abundance

Intercept	-1.800676E+00			
D100	5.426118E-03	Y	9.178E+00	1.361E+01
D500	2.401678E-02	Y	2.133E+01	1.666E+01
D1000	1.613741E-02	Y	2.175E+01	1.454E+01
D1000sq	3.635851E-03	Y	6.800E+02	8.264E+02
NDVI	-1.143232E-01	Y	5.004E-01	6.178E-02
Bri	-3.506220E-02	Y	-6.481E-02	2.634E-02

CF500	-3.014037E-02	Y	8.607E-01	1.224E-01
SH500	1.537414E-02	Y	3.641E-02	3.717E-02
GR500	4.015630E-04	Y	1.817E-02	6.804E-02
MERI_500	9.778020E-05	Y	1.132E-02	3.167E-02
ASP_500	2.085969E-03	Y	1.211E-02	3.543E-02
TR12-24	-2.740939E-03	Y	8.481E-01	1.234E-01
TR24_500	-1.279831E-02	Y	3.081E-02	9.073E-02
CANmd500	-8.323905E-03	Y	5.549E-01	2.348E-01

Small mammal richness

Intercept	1.637108E+00			
D100	-8.152534E-03	Y	1.266E+01	1.734E+01
D500	2.173864E-02	Y	2.347E+01	1.893E+01
D1000	4.045057E-02	Y	2.306E+01	1.639E+01
D1000sq	-4.535927E-02	Y	7.967E+02	9.856E+02
NDVI	-1.718069E-03	Y	4.960E-01	6.762E-02
Bri	-3.035414E-03	Y	-6.479E-02	2.545E-02
CF500	-8.976098E-03	Y	8.555E-01	1.208E-01
SH500	3.037504E-02	Y	3.173E-02	3.532E-02
GR500	2.194369E-03	Y	2.041E-02	6.044E-02
MERI_500	-2.169836E-04	Y	9.793E-03	2.684E-02
ASP_500	1.737354E-03	Y	9.475E-03	2.980E-02
TR12-24	-1.219391E-02	Y	8.301E-01	1.302E-01
TR24_500	1.547607E-04	Y	4.058E-02	1.049E-01
CANmd500	-1.846192E-03	Y	5.062E-01	2.546E-01

ANTS

Ant species richness (site)

Intercept	1.017347E+01	
HLI3X3S	1.266265E-02	N
PPTMMS	-4.533903E-01	N
ASP3X3S	-4.672606E-01	N
GRE3X3S	7.722682E-02	N
IMP100MS	-3.848212E-02	N
DEV3X3S	4.563628E-03	N
CC100S	-8.122350E-01	N

Log-nesting ant abundance

Intercept	8.720420E+00	
HLI3X3S	-9.439528E-01	N
PPTMMS	-9.772881E-02	N
NDVI3X3S	6.094930E+00	N
GRE3X3S	-2.045624E+00	N
DEV3X3S	6.918628E-01	N
DEV1000S	1.183739E+00	N
CC100S	-3.676185E+00	N

Thatch-nesting ant abundance

Intercept	3.434123E+00

HLI3X3S	1.170364E+00	N
PPTMMS	-1.396613E+00	N
NDVI3X3S	-7.934596E+00	N
GRE3X3S	9.108163E+00	N
DEV3X3S	4.348595E-01	N
DEV1000S	-2.140186E-01	N
JPN100S	-5.489477E-01	N

***Formica ravida* abundance**

Intercept	3.272263E-02	
HLI3X3S	1.649095E-03	N
PPTMMS	-1.900984E-02	N
NDVI3X3S	1.136876E-04	N
GRE3X3S	4.487378E-04	N
IMP100MS	8.622773E-05	N
DEV3X3S	6.868143E-04	N
CC100S	9.804777E-05	N

***Camponotus modoc* abundance**

Intercept	3.725244E-01	
HLI3X3S	-1.471251E-02	N
PPTMMS	8.421203E-02	N
NDVI3X3S	2.986735E-01	N
GRE3X3S	-1.471438E-01	N
IMP100MS	-1.497120E-03	N
DEV3X3S	6.516245E-03	N
DEV1000S	1.188077E-02	N

***Formica microphthalma* abundance**

Intercept	3.049150E-02	
PPTMMS	4.055748E-04	N
ASP3X3S	-1.670709E-04	N
NDVI3X3S	-9.676666E-04	N
GRE3X3S	-2.114181E-03	N
DEV3X3S	-2.181720E-04	N
DEV1000S	4.182702E-04	N
JPN100S	8.660841E-04	N

PLANTS

Exotic plant species richness

Appendix 9.1 – Table of basic relationships observed between measures of urbanization and associated habitat changes and measures of biological diversity.

Birds

Biodiversity metric	Percent development	Human activity	Snag volume	Canopy cover	Tree density	Herb & shrub cover	Comment
Total species richness	↘	↘					
Total abundance	↔ ⌒	↗					Relationship with percent develop on scale, 300m or 1km, respectivel
Community dominance	↗	↗					
Ground-nester abundance	↘	↘				↗	
Cavity-nester abundance	↘	↘	↗				
Invertivore abundance	↘	↘	↗	↗	↘		
Ground-foraging-omnivore abundance	⌒	↗					
Ground-nester richness	↘	↘					
Cavity-nester richness	↘	↘					
Nest success of all cavity nesters	↘						
Nest success of all open nesters	↘						
Nest success of ground nesters	↘						
Nest success of shrub nesters	↘						
Nest success of understory nesters	↘						
Steller's Jay nest success	↘						
Mountain Chickadee nest success	↔						
Dark-eyed Junco nest success	↘						
Dusky Flycatcher nest success	↘						Increase in nest success to 6% deve small sample size); did not nest ab
Pygmy Nuthatch nest success (2003)	↘						
Pygmy Nuthatch nest success (2004)	↔						
White-headed Woodpecker nest success	↔						

Western Wood-pewee nest success	↗	But nested lower to ground in high development, and success was lowe nests
American Robin nest success	↔	
Northern Flicker nest success	↔	
Red-breasted Nuthatch nest success	↔	
Abundance of 25 species	↘	Based on simple correlations; some relationships might be masked
Abundance of 28 species	↔	Based on simple correlations; some relationships might be masked
Abundance of 14 species	↗	Based on simple correlations; some relationships might be masked

Small Mammals

	Development and human disturbance metric				
Biodiversity metric	**% developed area**	**Human activity**	**Dog activity**	**Habitat heterogeneity**	**% cover bare ground**
Small mammal species richness	↗	↗	↔	↗	↗
Total small mammal relative abundance	↗	↘	↔	↗	↗
Arboreal squirrel abundance	↗	↔	↘	↗	↔
Terrestrial granivore abundance	↔	↔	↔	↔	↗
Terrestrial herbivore abundance	↗	↔	↔	↔	↔
Insectivore abundance	↔	↔	↔	↔	↔
Survival rate of long-eared chipmunks	↔	↔	↔	------	------
Survival rate of yellow-pine chipmunks	↔	↔	↔	------	------
Survival rate of shadow chipmunks	↘	↗	↗	------	------
Survival rate of lodgepole chipmunks	↘	↘	↘	------	------
Survival rate of golden-mantled ground squirrels	↘	↔	↔	------	------
Survival rate of California ground squirrels	↘	↔	↔	------	------
Survival rate of Douglas squirrels	↘	↔	↔	------	------
Emigration rates of long-eared chipmunks	↗	↔	↔	------	------
Emigration rate of golden-mantled ground squirrels	↗	↔	↔	------	------
Emigration rate of California ground squirrels	↔	↔	↔	------	------

Carnivores

Biodiversity metric	Dev_100	Dev_300	Dev_500	Dev_1000	People	Dogs	Vehicles	Vol_CWD	S
Herbivore richness	↘	↗	↘	↔	↗	↘	↘	↗	
Rabbit/hare occurrence	↘	↗	↘	↗	↗	↘	↘	↘	
Deer occurrence	↘	↗	↗	↘	↗	↘	↔	↗	
Carnivore richness	↘	↗	↘	↗	↘	↔	↘	↗	
Marten occurrence	↔	↘	↗	↘	↘	↔	↘	↗	
Black bear occurrence	↘	↗	↔	↔	↘	↘	↘	↔	
Coyote occurrence	↗	↗	↔	↗	↗	↔	↘	↘	

Plants

	Development at 300m	
Plant characteristics	**Undeveloped forest**	**Landscape-at-large**
Snag volume	↘	↘
Snag decay class	↘	↘
Log volume	↘	n.a.
Exotic plant species richness	↗	n.a.
Native plant species richness	↔	n.a.
Small diameter tree density	↘	↘
Medium diameter tree density	↔	↘
Shrub cover	↔	↘
Canopy cover	↔	↘
Decadence features	↔	n.a.
Stumps	↗	n.a.

Human Use

Use metric	**Dev_300**
Human Use	↗
Number of dogs	↗
Number of unleashed dogs	↘
Number of vehicles	↗