

## RESPONSE OF BROWN CREEPERS TO ELEVATION AND FOREST EDGES IN THE SOUTHERN SIERRA NEVADA, CALIFORNIA

KATHRYN L. PURCELL<sup>1</sup>, CRAIG M. THOMPSON, AND DOUGLAS A. DRYNAN<sup>2</sup>

USDA Forest Service, Pacific Southwest Research Station, 2081 E. Sierra Avenue, Fresno, CA 93710

**Abstract.** We studied the responses of the Brown Creeper (*Certhia americana*) to forest edges in the southern Sierra Nevada, California. We censused birds and monitored nests in four forest types over an elevational gradient. We identified habitat patches homogeneous in terms of forest type, seral stage, and canopy cover and rated edges between adjoining patches as soft, moderate, or hard on the basis of relative differences in the suitability of adjacent patches. Brown Creepers were more abundant in sites with less high-contrast edge and more medium- and high-quality habitat. They avoided soft and moderate edges when selecting nest sites. Successful nests were in large-diameter trees and snags in forest with lower canopy closure and farther from moderate and hard edges than were unsuccessful nests. Clear negative responses to edge in terms of abundance, nest location, and nest survival were surprising because previous work has suggested that edge effects and the processes underlying them may differ in western coniferous forests because of their natural heterogeneity and because past forest management in the region resulted in fairly soft edges. The strength of the response was somewhat tied to the severity of the edge, although creepers avoided even soft edges. Hard edges were relatively rare and resulted primarily from natural discontinuities. Our results suggest that Brown Creepers should benefit from forest management that retains mature forest with minimal discontinuities, regardless of their source. Results also suggest that differences in relative habitat quality rather than differences in vegetation were responsible for observed patterns.

**Key words:** Brown Creeper, *Certhia americana*, contrast-weighted edge, edge effects, elevational gradient, nest survival, snags.

### Respuesta de *Certhia americana* a la Elevación y a los Bordos de Bosque en el Sur de Sierra Nevada, California

**Resumen.** Estudiamos las respuestas de *Certhia americana* a los bordes de bosque en el sur de Sierra Nevada, California. Censamos las aves y monitoreamos los nidos en cuatro tipos de bosque a lo largo de un gradiente de elevación. Identificamos parches de hábitat homogéneos en términos de tipo de bosque, estadio seral y cobertura del dosel y categorizamos los bordes entre parches adjuntos como suave, moderado y duro en base a las diferencias relativas en cuanto a la aptitud de los parches adyacentes. Los individuos de *Certhia americana* fueron más abundantes en los sitios con menor contraste de borde y con calidad de hábitat media o alta. Evitaron los bordes suaves o moderados para la selección de los sitios de anidación. Los nidos exitosos se ubicaron en árboles de gran diámetro en bosques con menor cobertura del dosel y más alejados de bordes moderados y duros que los nidos sin éxito. Las respuestas negativas claras al borde en términos de abundancia, localización del nido y supervivencia del nido fueron sorprendentes porque los trabajos previos han sugerido que los efectos de borde y sus procesos subyacentes pueden diferir en los bosques de coníferas del oeste debido a su heterogeneidad natural y a que el manejo pasado del bosque en la región generó bordes bastante suaves. La fuerza de la respuesta estuvo de alguna manera atada a la severidad del borde, aunque los individuos de *C. americana* evitaron incluso los bordes suaves. Los bordes duros fueron relativamente raros y fueron el resultado principalmente de discontinuidades naturales. Nuestros resultados sugieren que *C. americana* podría beneficiarse de un manejo del bosque que mantenga los bosques maduros con mínimas discontinuidades, sin importar su fuente. Los resultados también sugieren que las diferencias en la calidad relativa de hábitat más que las diferencias en la vegetación fueron las responsables de los patrones observados.

## INTRODUCTION

Changes in landscape mosaics resulting from human activities have received much attention and have been linked to population declines and losses in biodiversity worldwide (Wilcove et al. 1986, Noss and Cooperrider 1994). A great deal of research

has focused on understanding the ecological patterns and processes responsible, much of it centered on the influence of fragmentation and habitat edges on wildlife species. While their affects can be similar, fragmentation and edges influence ecological processes in different ways and at different spatial scales (Fletcher et al. 2007). As continuous patches of

Manuscript received 15 September 2010; accepted 17 September 2011.

<sup>1</sup>E-mail: [kpurcell@fs.fed.us](mailto:kpurcell@fs.fed.us)

<sup>2</sup>Current address: H. T. Harvey and Associates, 7815 N. Palm Avenue, Suite 310, Fresno, CA 93711

habitat are broken down into smaller patches, the landscape becomes more fragmented and the amount of edge habitat is increased. The implications of increases in edge habitat for bird populations are numerous and include alteration of microclimates, changes in vegetation structure and composition, and changes in the abundance of prey, predators, and brood parasites (Brand and George 2001, Sisk and Battin 2002).

Ecological thinking on edges has undergone dramatic changes since the concept was first introduced. Initially, edges were associated with elevated abundance and diversity of plants and animals and were considered beneficial features of landscapes (Leopold 1933, Lay 1938, Johnston 1947). The view that edges were beneficial changed when avian ecologists began finding increased levels of nest predation and brood parasitism close to forest edges, which led to a fundamental shift in our view of edge effects (Gates and Gysel 1978, Wilcove et al. 1986, Paton 1994, Andrén 1995). The generality of these conclusions began to be questioned, however, as accumulating studies began showing inconsistent results, with species varying in their responses to edges and types of edges (Andrén 1995, Donovan et al. 1997, Lahti 2001). Response to edges may depend on edge type, orientation, edge contrast, landscape context, the predator community, and the effects of parasitism (Donovan et al. 1997, Tewksbury et al. 1998, Ries et al. 2004). Recent efforts to provide a predictive framework to help clarify the patterns and variability observed suggest that responses to specific types of edges are predictable on the basis of patterns of resource distribution and use by each species (Ries and Sisk 2004, Ries et al. 2004).

Several biases exist in the literature on habitat edges and their effects. Most studies have examined forest edges, with forest/agricultural edges most commonly studied (Wilcove et al. 1986, Paton 1994, Andrén 1995). In addition, there has been a geographic bias toward studies done in eastern North America (Paton 1994, Sisk and Battin 2002). Most studies have focused on edges resulting from anthropogenic activities, and the influence of edges resulting from natural heterogeneity has received little attention (Paton 1994). The relative importance of human-caused changes in landscape mosaics versus those resulting from natural ecological processes may vary geographically as a result of differences in management history, historical processes, and landscape context (Rosenberg et al. 1999, George and Dobkin 2002).

How edges are defined is a critical first step in studying edge effects. Following Ries and Sisk (2010), we defined an edge as the boundary between two vegetation-cover classes. Because edges are boundaries between patches differing in vegetation, identification of edges depends on how patches are defined (Strayer et al. 2003, Ries et al. 2004). Minimum patch size is an important consideration because small patches may be completely influenced by edge effects. On the basis of microclimatic conditions within openings, Paton (1994) suggested that only openings in the forest canopy with a diameter at least three times the height of adjacent trees should

be included in edge analyses. Wilkin et al. (2007) considered only clearings exceeding 0.5 ha. Patches are most often delineated from vegetation maps such as GIS coverages based on aerial photographs and other sources to define stand boundaries and therefore edges (e.g., Brittingham and Temple 1983, Hawrot and Niemi 1996, Tewksbury et al. 1998).

Most edge studies have investigated relationships between animal distributions and edges resulting from differences in vegetation structure, such as vegetation height or density (Ries et al. 2004). Avian ecologists have most often defined patches as areas differing in vegetation structure and composition, but patches can also be defined as areas differing in resources, habitat quality, or other factors that influence ecological processes (Strayer et al. 2003, Ries and Sisk 2004). We utilized this second approach, defining habitat quality as the ability of the environment to provide conditions appropriate for persistence of individuals and populations (Hall et al. 1997), linking it explicitly with habitat features associated with productivity.

Edges vary in their abruptness, and species may vary in their responses to edges with varying degrees of contrast (Hawrot and Niemi 1996). Edge effects are expected to be greater near high-contrast edges where differences between adjacent patches are greater than at low-contrast edges, but few studies have looked at the differing effects of edges of varying degrees of contrast.

Understanding responses to habitat heterogeneity is important for identifying the resources necessary for population persistence, and a better understanding of species' responses to habitat edges is needed. As changes in landscapes due to forest management continue, the type and amount of edge will change as well (Hawrot and Niemi 1996). This is true especially in western conifer forests, which differ in several ways from the better-studied eastern landscapes. Western landscapes have more natural heterogeneity, and we need to understand how species respond to both natural and anthropogenic edges. Information is also needed on how species respond to edges differing in contrast. Management techniques in western forests have generally shifted from even-aged management techniques, such as clearcutting, which creates abrupt edges and large patches, to uneven-aged management, which results in softer edges and smaller patches.

The Brown Creeper (*Certhia americana*) is widely distributed in coniferous forests in North America, but little is known of key aspects of its breeding ecology. Brown Creepers favor closed-canopy forests with a high density of large trees for nesting (Hejl et al. 2002a). The species is generally considered a forest-interior specialist that avoids edges (Whitcomb et al. 1981, Rosenberg and Raphael 1986, Nelson 1988, Freemark and Collins 1992, Brand and George 2001, but see Mayrhofer 2006), although studies examining forest fragmentation and area requirements have shown inconsistent responses. Partners in Flight groups are concerned about the Brown Creeper in Washington, Oregon, Idaho, Montana, and California (Hejl et al. 2002a).

The list of research needs in the California Partners in Flight Coniferous Forest Bird Conservation Plan (CalPIF 2002) includes the need for information on the characteristics of high-quality habitat, how landscape factors and management practices affect the creeper's productivity, and the effects of fragmentation on its nest productivity.

We studied the edge responses of Brown Creepers breeding in four forest types over an elevational gradient in the Sierra Nevada of California. We examined the species' responses to forest edges in western coniferous forests by testing for differences in abundance, nest placement, and reproductive success in relation to edges varying in contrast. We also explored its selection of breeding habitat by investigating local and landscape-level factors affecting abundance and reproductive success.

## METHODS

### STUDY AREAS

We studied Brown Creepers in four forest types along an elevational gradient in the High Sierra Ranger District of Sierra National Forest on the western slope of the southern Sierra Nevada. In order of increasing elevation, the forest types were ponderosa pine (elevation 1024–1372 m), mixed conifer (1707–2012 m), true fir (2170–2347 m), and lodgepole pine (2469–2774 m). Dominant tree species in the ponderosa pine sites included ponderosa pine (*Pinus ponderosa*) and incense cedar (*Calocedrus decurrens*). Mixed-conifer sites were dominated by white fir (*Abies concolor*) and incense cedar, true fir sites were dominated by white fir and red fir (*A. magnifica*), and lodgepole pine sites were made up almost exclusively of lodgepole pine (*P. contorta*).

We established 18 study sites, four sites in each forest type except for mixed conifer, where there were six. Of the six mixed-conifer sites, we sampled four each year on a rotating schedule, such that each site was sampled an equal number of years over the study. Each site consisted of at least 60 ha of mature forest with relatively high canopy cover. To facilitate censusing and mapping and relocation of nests, we established a 40-ha gridded plot at each of the sites. The 40-ha plot generally included forested areas with large trees and high canopy cover, although natural heterogeneity resulted in all plots having some open rocky or brushy areas and small meadows or streams. We established a 1000-m transect within the 40-ha plot to facilitate bird censuses. Transects were situated primarily in the targeted habitat (mature forest with high canopy cover) and most often consisted of two segments separated by a minimum distance of 250 m (when parallel).

### FIELD WORK

From 1995 to 2002, we censused birds on 8 (1995) or 16 (1996–2002) plots by using a timed transect method. Observers walked the 1000-m transect at a rate of 50 m per 3 min, recording all birds seen or heard within 50 m of the transect line and those detected at unlimited distance but still within the

study site. Each site was visited six times per season by three to four observers each year. Observers were carefully selected for proficiency in bird identification by sight and sound. All observers visited each site an equal number of times each year, and we retained observers for as many years as possible to help control for observer variability. Surveys were completed between 17 April and 16 May at ponderosa pine sites, 22 May and 15 June at mixed-conifer sites, 5 June and 6 July at true-fir sites, and 21 June and 25 July in lodgepole pine sites. We scheduled surveys to coincide with the peak singing period for most species in each forest type; hence higher sites were sampled later in the year. We selected the order of visits to plots and starting points within plots randomly with the constraint that visits were evenly divided between the two starting points. We began surveys at 07:00 PDT in all forest types except ponderosa pine, where counting began at 07:30 PDT to accommodate shorter days earlier in the season.

We searched for nests throughout each site every year by using behavioral cues such as carrying nesting material or food and following birds to their nests. In each forest type, nest searches were begun when nests were being initiated and continued through the nesting period. We monitored nests every 3 or 4 days until either the young fledged or the nest failed. Where possible, we checked nest contents once a week by climbing to the nest, using a fiberscope or a mirror to view nest contents (Purcell 1997). For nests observed directly, we recorded the number of eggs and nestlings and the appearance of the nestlings. During the early stages of nesting and when nests were in substrates that were difficult or hazardous to climb, we observed nests from the ground, noting the presence and behavior of adults and the appearance of the nests. Nests were occasionally found in the same snag or tree in subsequent years; we used data from the first nesting attempt only in analyses. We assumed predation when eggs or nestlings too young to have fledged disappeared from the nest.

We determined a nest's age by extrapolation from identified events such as the beginning of incubation, hatching, or fledging. In addition, descriptions of known-aged nestlings from this study were helpful in aging nestlings and determining nest fate. We excluded from analysis nests whose age we were unable to determine ( $n = 17$ ).

On the basis of average values from nests with complete information for a particular period, the incubation and nestling periods both averaged 15 days ( $n = 35$  for incubation and  $n = 51$  for nestling). We used the average clutch size ( $4.9 \pm 0.2$  SE,  $n = 13$ ) to determine the duration of the laying phase, subtracting one day for the beginning of incubation and assuming one egg was laid per day (4 days). We found no evidence that incubation and nestling periods differed by forest type ( $F_{3,31} = 1.50$ ,  $P = 0.23$  for incubation and  $F_{3,47} = 1.87$ ,  $P = 0.15$  for nestling). Thus for calculating nesting success we used 34 days as the length of a successful nesting attempt.

Following the breeding season, we measured characteristics of each nest and its habitat, including nest height, substrate

species and diameter at breast height (dbh), and canopy closure (measured with a concave spherical densiometer). For canopy closure, we took four readings at the base of the nest tree, turning 90° between readings and avoiding inclusion of the bole and canopy lower than 5 m. We averaged the four readings.

We used a GIS vegetation layer provided by the Sierra National Forest to generate GIS coverages of each study plot, including a 1-km buffer around the perimeter of each plot. The vegetation layer consisted of stand-level data, collected by USDA Forest Service personnel, and corrected by aerial-photo interpretation. This resulted in a polygon coverage, where polygons represented patches of homogeneous habitat between 0.5 to 400 ha. We assigned habitat-quality values to each polygon according to the California Wildlife Habitat Relationships (CWHR) database, a matrix-based model of wildlife-habitat relationships developed from the literature and scientific opinion for each species of terrestrial vertebrate in California (<http://www.dfg.ca.gov/biogeodata/cwhr/>; see Appendix). CWHR habitat classifications are based on habitat type, tree size, and canopy cover. The CWHR database rates each habitat's suitability for reproduction, cover, and feeding and assigns each habitat type/tree size/canopy cover combination a habitat-suitability rating of high, medium, low, or unsuitable. For our analysis, we used habitat-suitability ratings for reproduction.

We examined three types of edges: soft, moderate, and hard. Edge types were based on the degree of change in CWHR habitat-suitability ratings between adjacent patches. Soft edges were defined by one degree of change. In other words, they occurred at edges between patches rated unsuitable and low, low and medium, or medium and high. Moderate edges had

two degrees of change, or where patches rated as unsuitable and medium or as low and high abutted. Hard edges, defined by three degrees of change, were restricted to the transition between unsuitable and high-quality habitat. Note that patches of low and medium suitability could not have a hard edge.

We digitized nest locations from gridded maps of each study site and overlaid them on the GIS vegetation layer. We classified the accuracy of digitized nest locations as high (within 5–10 m), medium (within 25 m), or low (within 100 m). We relocated nests with locations of medium and low accuracy in 2008 and 2009 and recorded accurate locations (<10 m) with a hand-held GPS unit. In a few cases nest locations could not be identified with confidence; these nests were not used in spatial analyses. We measured distance to the nearest edge for nest locations and for 50 random points per plot (900 total). Random points were generated by Hawth's Tools extension in ArcGIS (Beyer 2004) and did not coincide with nests (average distance from a nest to the nearest random location was 173.80 m, range 5.93–724.03 m).

#### STATISTICAL ANALYSIS

*Abundance and landscape configuration.* We selected eight variables related to fragmentation and edge effects to test whether the Brown Creeper's abundance was related to landscape configuration (Table 1). We used FRAGSTATS (McGarigal and Marks 1995) to calculate the eight variables for each of the 18 study plots. To assign weights for contrast-weighted edge density, we used values of 0.33, 0.66, and 1.00 for soft, moderate, and hard edges, respectively. We used forward stepwise regression to identify important metrics, with the

TABLE 1. Definition of FRAGSTATS variables used in analysis and mean values for 18 study sites for the Brown Creeper in the southern Sierra Nevada, California.

Variable	Definition	Mean $\pm$ SD
% Landscape 3/4	Percent of landscape defined by CWHR as high- or medium-quality breeding habitat.	90.81 $\pm$ 8.64
% Landscape core	Percent of landscape that meets the definition of CWHR high- and medium-quality breeding habitat (PLand3/4) and of a core area. Core area is defined as the internal patch area, at least 50 m from any edge.	29.06 $\pm$ 20.11
Number of disjunct patches	Total number of patches, of any kind, within the landscape. An index of overall landscape fragmentation.	13.77 $\pm$ 9.55
Largest patch index	The percent of the landscape contained in the single largest patch of CWHR high- or medium-quality breeding habitat. It equals 100 when the landscape is a single large patch and approaches zero as the size of the largest patch decreases.	78.25 $\pm$ 20.19
Number of disjunct core areas	Total number of core areas, defined as a patch $\geq$ 50 m from an edge of CWHR high- or medium-quality breeding habitat.	3.11 $\pm$ 2.03
Contrast-weighted edge density	Meters of edge per hectare, weighted by the degree of contrast. Equals zero when the landscape is a single patch (i.e., no edge) and increases with more edge and/or greater contrast.	53.00 $\pm$ 32.35
Contagion	The abundance of each patch type multiplied by the proportion of "like adjacencies," or how often two cells of a similar habitat type are located next to one another. Inversely related to edge density. Approaches zero as cells are maximally disaggregated and interspersed. Equals 100 when cells are maximally aggregated (i.e., the landscape is a single patch.)	76.14 $\pm$ 12.46
Shannon's diversity index	Diversity of patch types present on the landscape. Equals zero in a homogeneous landscape and increases as the number of different patch types increases and/or the proportional distribution of area among patch types becomes more even.	0.53 $\pm$ 0.33



number of Brown Creepers detected per plot (unlimited distance) as the response variable (Penhollow and Stauffer 2000, Kumar et al. 2006). Proc REG (SAS Institute 2002) was used for the stepwise regressions, with  $P < 0.20$  to enter the model.

*Nest location and edge effects.* We used *t*-tests to assess differences in mean distance to the three edge types for nests and random points. We hypothesized that nests should be farther from edges than should random points and therefore used one-tailed *t*-tests to compare distances of nests and random points (SAS Institute 2002). We tested for equality of variances with Levene's test. Because birds are unlikely to respond to edges that are far from their nests and territories, we considered only edges  $\leq 150$  m from nests in analysis of nest locations, basing this cutoff on the following reasoning. Territory-mapping data from one of the mixed-conifer sites studied here and a transitional mixed-conifer/true-fir site suggested conservative territory sizes of 16 and 11.6 ha, respectively (Purcell, unpubl. data), yielding diameters of 143 and 122 m (conservatively assuming territories are round). Two studies of breeding Brown Creepers in California reported densities ranging from 4.8 to 50 pairs per 40 ha, yielding territory sizes of 0.80 to 8.33 ha and territory diameters from 101 to 324 m ( $\bar{x} = 185$  m,  $n = 7$ ; Beedy 1981, Raphael and White 1984). We excluded from comparisons nests and random locations that didn't have an edge of a particular type (soft, moderate, hard) within 150 m.

*Nest survival.* We used the logistic exposure method (Shaffer 2004) to examine whether nest survival was influenced by habitat characteristics and Akaike's information criterion, corrected for small sample size, to rank candidate models. We first evaluated effects of nest age, date, and year to control for potentially confounding effects of time-specific factors. We considered models that included linear, quadratic, and cubic effects of nest age, linear and quadratic effects of date, and a categorical effect of year (Grant et al. 2005). A cubic effect of age is plausible if survival through the egg-laying, incubation, and nestling stages differs. Quadratic effects of date are plausible if nest survival is higher or lower midseason. Quadratic and cubic models included all lower-order terms. The 24 models evaluated included a model of constant daily survival (null model) and all combinations of age, date, and year effects. We included the most-supported time-specific model in subsequent analyses.

To evaluate the influence of nesting-habitat characteristics and edge effects on nest survival, we examined models including nest height, substrate dbh, canopy closure, and edge types. Because patches of low and medium habitat suitability could not have a hard edge, we examined distance to soft edge, distance to moderate edge, and distance to moderate or hard edge, whichever was closer. We used the nearest edge rather than restricting observations to edges within 150 m as a conservative measure of the importance of edge effects. We hypothesized that successful nests should be higher, in larger trees and snags, in areas of higher canopy closure, and farther from high-contrast edges. Only one edge type was included

in any model and, because nest height and substrate diameter were correlated ( $r = 0.44$ ,  $P < 0.0001$ ), they were not included in the same model. We tested a total of 24 models, including the most-supported time-specific model as the base model.

We evaluated goodness of fit by following Sturdivant et al. (2007). Because two of the nesting-habitat variables were correlated (nest height and substrate diameter) and only one of these and only one edge-distance variable was tested in any one model, there was no true global model for nesting-habitat characteristics and no unique most-parameterized model. We applied goodness-of-fit tests to the most-supported model, which also had the maximum number of parameters ( $K = 4$ ).

## RESULTS

### ABUNDANCE

Patterns based on detections within 50 m and unlimited-distance detections were similar (Fig. 1a). Although Brown Creepers occurred in all four forest types along the elevational gradient, their abundance varied. Brown Creepers were most abundant at high-elevation lodgepole pine sites and least abundant at low-elevation ponderosa pine sites.

Two variables, contrast-weighted edge density and the percent of landscape in high- and medium-quality habitat, were associated with Brown Creeper abundance (Table 2). Plots that supported higher numbers of birds had smaller amounts of high-contrast edges and more habitat defined as of high and medium quality for reproduction. The latter is typically mature and late-seral coniferous forest with moderate to dense canopy cover (see Appendix). None of the variables describing fragmentation or patch size entered the model. Univariate regressions indicated no relationships between the remaining landscape variables and creeper abundance ( $R^2 = 0.01$  to  $0.07$ ,  $P = 0.32$  to  $0.67$ ,  $df = 16$ ).

### NEST SITES

We located and monitored 224 nests from 1995 through 2002 ( $n = 28, 57, 27$ , and  $112$  in ponderosa pine, mixed conifer, true fir, and lodgepole pine, respectively). Twelve nest sites were reused in a subsequent year. Most nests (93%) were in snags. Nests were in a wide variety of tree species, but some patterns were evident. At ponderosa pine sites 81% of nests were in ponderosa pine trees or snags, at mixed-conifer sites 60% were in sugar pine (*Pinus lambertiana*), at true-fir sites 68% were in red or white fir, and at lodgepole pine sites 94% were in lodgepole pine. Of nests in live trees, slightly more than half (8 of 14) were in incense cedars, in small natural cavities formed in or behind the rugged, deeply furrowed bark of healthy trees.

As hypothesized, Brown Creepers nested at distances farther from soft and moderate edges ( $t_{469} = 1.9$ ,  $P = 0.027$  for soft edges;  $t_{350} = 2.6$ ,  $P = 0.005$  for moderate edges) than were random points (Fig. 2). Distance to hard edges did not differ ( $t_{265} = 0.6$ ,  $P = 0.283$ ), although the difference was in the expected direction. Hard edges within 150 m of a nest were relatively rare.

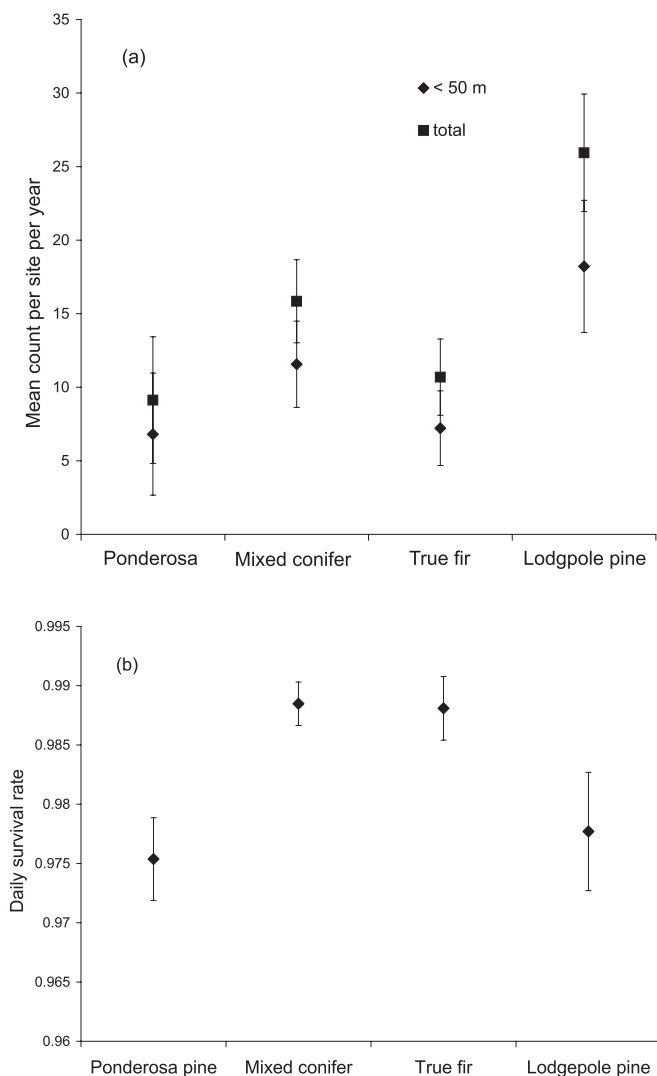


FIGURE 1. Abundance (a) and daily nest-survival rates (b) of Brown Creepers in four forest types over an elevational gradient in the southern Sierra Nevada, California. Abundance includes detections within 50 m and at unlimited distance per site averaged over the eight years of the study. Sample sizes for nesting success were 27, 52, 26, and 107 for ponderosa pine, mixed conifer, true fir, and lodgepole pine, respectively. Error bars represent 95% confidence intervals.

#### NESTING SUCCESS

Overall nesting success was 58% but was lower at low-elevation ponderosa pine sites (43%) than at mid-elevation mixed-conifer and true-fir sites (67% for each). Nesting success in high-elevation lodgepole pine (46%) was low but

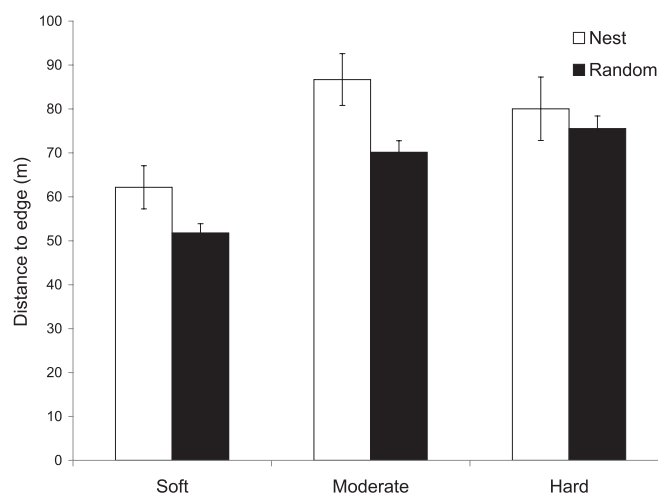


FIGURE 2. Distance to soft, moderate, and hard edges from Brown Creeper nests ( $n = 71, 61,$  and  $36$  for soft, moderate, and hard edges, respectively) and random points ( $n = 398, 291,$  and  $231$ ). Error bars represent 1 SE. Only edges within 150 m of the nest or random point were considered. See Table 1 for definitions of edge types.

variable, and confidence intervals for daily nest survival overlapped those of the other forest types (Fig. 1b). Most nest failures were due to predation, but three nests were abandoned with eggs and three were lost because of structural failure.

For the time-specific models, no one model accounted for a majority of the Akaike weight and four models had  $\Delta AIC_c < 2$ , including the null model (Table 3). The 95% confidence intervals for all parameter estimates included zero, indicating that they had minimal biological effect. Linear and quadratic effects of age and date were uninformative parameters that did not explain enough variation to justify their inclusion (Burnham and Anderson 2002, Arnold 2010). Thus no time-specific variables or models were included in the models of nesting habitat.

The most-supported nesting-habitat model included substrate diameter, canopy closure, and distance to moderate or hard edge and accounted for 59% of the Akaike weight (Table 3). No other models were within 2  $\Delta AIC_c$  units. None of the 95% confidence intervals for the parameter estimates included zero, indicating that all of the parameters contributed to the fit of the data (Table 4). Goodness-of-fit statistics indicated that the best-supported model fit the data ( $P = 0.83$ ). Survival was higher in nests in larger snags and trees, with lower canopy closure, and farther from moderate or hard edges (Table 4, Fig. 3).

TABLE 2. Results of stepwise forward regression to identify landscape-configuration variables important for predicting Brown Creeper abundance in the southern Sierra Nevada, California. See Table 1 for definitions of variables;  $n = 18$  study sites.

Step	Variable	Partial $R^2$	Model $R^2$	$F$	$P$
1	% Landscape 3/4	0.119	0.119	2.15	0.1618
2	Contrast-weighted edge density	0.530	0.649	22.62	0.0003

TABLE 3. Selection results for models explaining variation in survival of Brown Creeper nests in the southern Sierra Nevada, California. Time-specific effects were examined first to control for effects of nest age (linear, quadratic, and cubic effects), date (linear and quadratic effects) and year. The 24 nesting-habitat models examined include combinations of nest height, substrate diameter at breast height, percent canopy closure, distance to soft edge, distance to moderate edge, and distance to moderate or hard edge (see text). Models with quadratic and cubic included all lower-order terms.  $K$  is the number of parameters in the model,  $AIC_c$  is Akaike's information criterion for small samples,  $\Delta AIC_c$  is the scaled value of  $AIC_c$ , and  $w_i$  is the Akaike weight. Models shown here are those with  $\Delta AIC_c \leq 2.0$  for time-specific models and  $\Delta AIC_c \leq 4.0$  for nesting-habitat models. Effective sample size was 3000 exposure days.

Model	$K^a$	$\Delta AIC_c$	$w_i^b$
Time-specific models			
Nest age <sup>c</sup>	2	0.0	0.21
Nest age <sup>2</sup>	3	1.3	0.11
Nest age + date	3	1.7	0.09
Null	1	1.7	0.09
Nesting habitat			
Substrate dbh + percent canopy closure + distance to moderate or hard edge <sup>d</sup>	4	0.0	0.59
Percent canopy closure + distance to moderate or hard edge	3	2.4	0.17
Nest height + percent canopy closure + distance to moderate or hard edge	4	3.4	0.11

<sup>a</sup>Number of estimable parameters

<sup>b</sup> $AIC_c$  model weight

<sup>c</sup>Minimum  $AIC_c = 277.1$ .

<sup>d</sup>Minimum  $AIC_c = 263.2$ .

## DISCUSSION

### RESPONSE TO EDGE

Brown Creepers breeding in the Sierra Nevada clearly responded to edges within a forest mosaic. We examined the effects of edge on abundance, nest location, and nest survival, and in all three cases found negative responses to edges. Brown Creepers were more abundant in plots with less high-contrast edge, nested farther from soft and moderate edges, and reproduced more successfully farther from moderate or hard edges.

Despite the fact that most previous studies have shown the Brown Creeper to be sensitive to edges (Rosenberg and Raphael 1986, Nelson 1988, Brand and George 2001, but see Mayrhofer 2006), this clear negative response to edges was surprising for two reasons. First, the effects of fragmentation and creation of edges on bird populations of western conifer forests may differ

intrinsically from those in eastern forests where the majority of studies have been done (Rosenberg et al. 1999, George and Dobkin 2002, Hejl et al. 2002b, Sisk and Battin 2002). In western North America forests are heterogeneous and naturally patchy because of varied topography and periodic disturbance by fire and other natural processes (Tewksbury et al. 1998, George and Dobkin 2002, Hejl et al. 2002b), and habitats in the relatively young and rugged Sierra Nevada are no exception. Edge effects, and the processes underlying them, may differ markedly in western landscapes (Sisk and Battin 2002). Birds of western forests may be less affected by fragmentation and other measures of landscape configuration because they have existed with the natural heterogeneity of western landscapes for thousands of years and may have evolved mechanisms for coping with interspecific interactions (McGarigal and McComb 1995, George and Dobkin 2002). On the other hand, a clear response to edges in western North American forests, such as we found here, could also be the result of prolonged exposure to landscape heterogeneity that helped promote specialization of species that inhabit those forests.

Second, our definition of edge was fairly conservative compared to that used in studies that have primarily examined much more abrupt edges such as those between uncut forests and recent clearcuts, agriculture, or urban areas. We studied edge effects within a forest mosaic with a silvicultural disturbance history of selective logging that targeted larger stems (McKelvey and Johnston 1992) and resulted in relatively soft edges. Soft edges were far more common across the landscape than were moderate or hard edges. Uncharacteristically, in our study area hard edges more often resulted from natural discontinuities such as edges between forest and meadows or rocky areas than from forest management. Historically, the distribution of edges in the Sierra Nevada helped maintain this diverse landscape by creating barriers to natural disturbance such as wildfire or insect outbreaks.

Most studies of avian response to habitats, in both eastern and western North America, have focused on anthropogenically generated edges. In many areas, western landscapes have been managed by even-aged techniques that resulted in landscapes dominated by trees of even ages and high-contrast, human-caused edges. In Douglas-fir forests in western Oregon, McGarigal and McComb (1995) found that high-contrast edges were common and most reflected boundaries between late-seral forests and young Douglas-fir plantations. They failed to detect find strong negative relationships between avian abundance

TABLE 4. Parameter estimates, standard errors, and 95% confidence intervals for the most-supported model explaining variation in nest survival of Brown Creepers in the Sierra Nevada. See Table 3 for definitions of variables.

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI
Substrate dbh	0.0140	0.0072	0.000	0.0281
Percent canopy closure	-0.0303	0.0114	-0.0527	-0.0079
Distance to moderate or hard edge	0.0044	0.0018	0.0009	0.0079

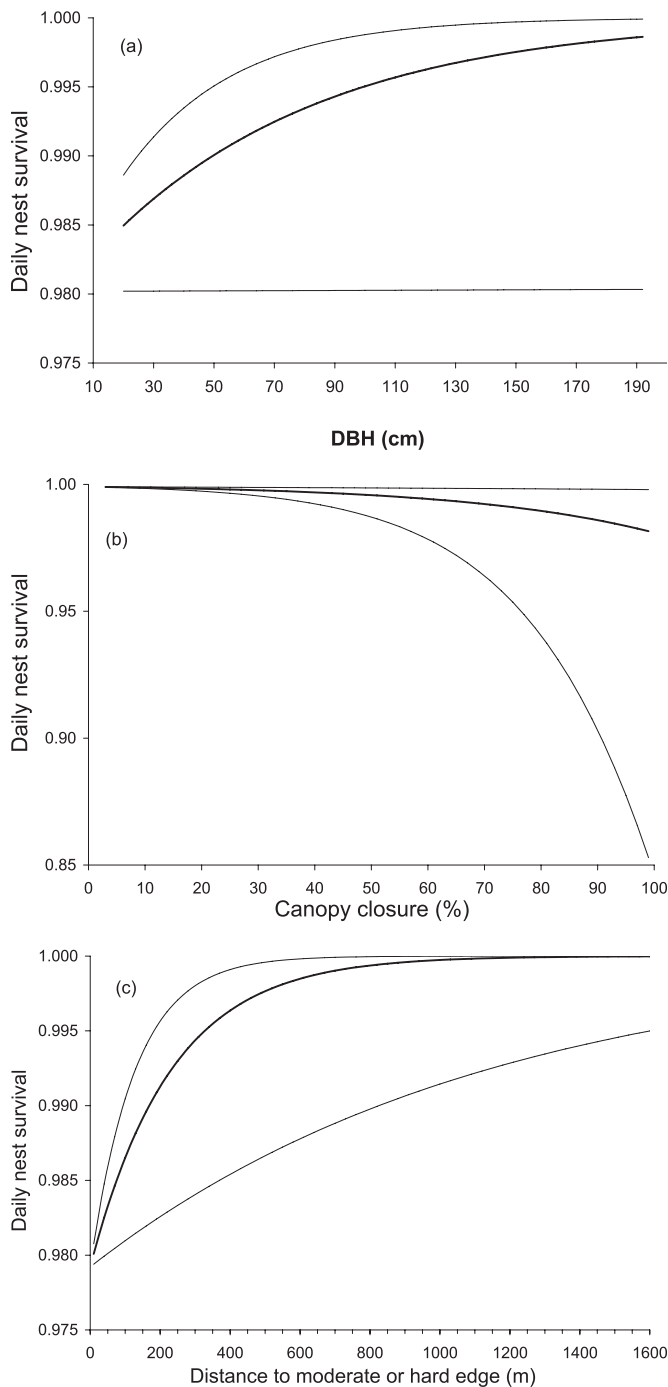


FIGURE 3. Rates of daily survival of Brown Creeper nests as a function of (a) nest-substrate diameter, (b) canopy closure, and (c) distance to moderate or hard edge. Estimates are based on the model  $\log(S/1 - S) = 5.042 + 0.014 \text{ substrate diameter} - 0.030 \text{ canopy closure} + 0.004 \text{ distance to moderate or hard edge}$ . Based on the range of values for the variable specified while all other variables were held constant at their mean value. Error bands represent 95% confidence intervals.

and landscape structure and concluded that landscape structure had only a moderate effect on bird abundance in the Oregon Coast Range. As did we, they found that Brown Creepers were strongly affected by the extent of late-seral forests, but, in

contrast, the species' relationships with habitat configuration were otherwise weak and inconsistent.

Edge contrast is most commonly defined by the degree of difference between adjoining patches in terms of vegetation structure and composition. As have most studies, we defined patch types based on vegetation characteristics, classifying patches by habitat type, seral stage (based on tree size), and canopy cover. But unlike most other studies, we defined contrast-weighted edge on the basis of the relative habitat quality of adjacent patches for the focal species, rather than simply by the degree to which bordering patches differed structurally. The indices of habitat quality we used assumed patches rated highly suitable for reproduction have the requisite resources for successful reproduction and will maximize fitness. The habitat-suitability ratings were developed independently of our data and represent associations generalized over all habitats in the Brown Creeper's California range. In addition to providing a test of the CWHR model (which appeared to perform well), our results provide evidence that relative habitat quality rather than simply change in vegetation is responsible for the edge responses we observed. Ries and Sisk (2004) presented a conceptual model that predicted whether species would increase, decrease, or remain unchanged at edges between adjacent patches that differed in habitat quality. Habitat quality was based on the relative availability of resources between the two patches, rather than on forest structure. Their model correctly predicted the direction of 83% of edge responses for 52 bird species. Similarly, Kristan et al. (2003) used habitat-suitability scores obtained from independently derived habitat models to test mechanistic explanations for differences observed in the distribution and abundance of bird and mammal species at urban-wildland edges.

Sensitivity to patch size and edge may be correlated because the relative amount of edge increases as patch size decreases, so that edge effects operate on a larger proportion of the area of small patches (Villard 1998). Patch size and edge effects are often confounded in study design, but nonconfounded studies have found support for edge effects more frequently (Fletcher et al. 2007). In our analysis of Brown Creeper abundance, we examined several landscape-configuration variables related to fragmentation, patch size and configuration, and edge. None of the variables representing habitat diversity or patch size or shape was important in describing variation in abundance. Only variables related to edge density and the overall amount of good breeding habitat were important in explaining variation in abundance.

The strength of the response was somewhat tied to the severity of the edge. Abundance was higher on sites with less high-contrast edge, and nests farther from moderate and hard edges had better survival, but the creepers avoided even soft edges when selecting nest sites. Hard edges were relatively rare across the landscape and resulted primarily from natural discontinuities rather than those resulting from forest management. Abundance was also higher at sites with more habitat suitable for reproduction. Taken together, these results suggest that Brown



Creepers should benefit from forest management that retains fairly large patches of continuous mature and late-seral forest with minimal discontinuities, regardless of their source.

Our study did not address mechanisms generating edge effects. Responses to edge may be related to a wide range of phenomena, including alterations in microclimate (leading to differences in soil and air temperature and moisture), vegetation structure and composition, differences in critical resources such as invertebrate abundance, and changes in interspecific interactions, such as competition, predation, and nest parasitism. Reduced avian reproductive success at edges has most often been attributed to higher rates of predation and brood parasitism (Gates and Gysel 1978, Brittingham and Temple 1983, Temple and Cary 1988). Brood parasitism is an unlikely factor for the Brown Creeper, which is an uncommon host of the Brown-headed Cowbird (*Molothrus ater*; Davis 1978, Friedmann and Kiff 1985). Nest predation near edges is a likely cause for our finding that nests near edges had reduced success, as nest predation was the primary cause of nest failure. Two other studies have found similar results. Mayrhofer (2006) found no difference in success (naïve estimates) between nests placed close to edges and nests far from edges when she considered only edges within 85 m of the nest, but when she extended this radius to 100 m, nests far from edges were significantly more successful than nests close to edges, although sample sizes were small. Kuitunen and Helle (1988) found that Common Treecreepers (*C. familiaris*) nesting in nest boxes experienced higher nest predation at forest margins (<20 m) than in forest interiors.

But other factors, such as food abundance and microclimate preferences might also be responsible, at least in part, for the differences in abundance and reproductive success we observed. Although populations of invertebrates are generally considered denser at edges than in interior forests (Helle and Muona 1985, Jokimäki et al. 1998), some evidence suggests that edges have lower abundances of the bark-dwelling invertebrates consumed by creepers. Duguay et al. (2000) found that the biomass of invertebrates that hide under tree bark such as those used by bark gleaners was lower in clearcut stands than in two-age stands and interior forest.

Brand (2004) analyzed ecological and life-history traits to predict edge responses of forest birds. She found that species more likely to respond negatively to edges between forest and open habitats included forest birds, birds associated with mesic habitats, bark foragers, insectivores, species with long nesting periods, long-distance migrants, species with smaller body mass, and more specialized species. Her model predicted negative edge responses by the Brown Creeper, a small insectivorous forest bird that forages on bark and is associated with mesic habitats (Hejl et al. 2002a).

#### ABUNDANCE, NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS

Brown Creepers were most abundant at high-elevation lodgepole pine sites but nested most successfully in mid-elevation conifer forests. At high elevations in lodgepole pine forests

where the species was most abundant, nest survival was variable, which was apparently unrelated to sample size. Variability in nest survival at high elevations could be due to the greater seasonality and lower predictability of the climate at high elevations (Boyce 1979). High-elevation habitats appear to be preferred over lower elevations even though the probability of successfully producing young is unpredictable.

Our results showing use of a wide variety of snag species are consistent with previous studies (e.g., Davis 1978, Bagne 2006). Species used for nesting coincided with the dominant tree species for each forest type except for mixed conifer, where relatively rare sugar pines were primarily used. The primary requirement for nest sites appears to be a space behind a loose piece of bark on a large, typically dead or dying tree. Site selection is important; we found that structural failure was a factor in nest survival, as did Davis (1978). We found that use of live trees was higher than reported in most studies (Hejl et al. 2002a) and use of natural cavities in incense cedar trees has not been reported elsewhere.

Nests in large-diameter trees and snags were more successful, and the relationship appeared to hold throughout the range of diameters used (up to 191 cm dbh). Suorsa et al. (2003, 2005) reported the closely related Eurasian Treecreeper to occupy forest patches with stems larger than in unoccupied patches. They also found that the density and size of suitable food items were higher on larger than on the smaller stems that the treecreepers preferred to forage on.

Our finding that nest survival decreased with increasing canopy closure was unexpected because other studies have found that creepers are more abundant in areas of high canopy cover (Verner and Boss 1980, Beedy 1981, Hejl and Verner 1988, Nelson 1988) and is surprising for a species considered to be a forest-interior specialist associated with late seral stages and a high density of large trees (Hejl et al. 2002a). The wide confidence intervals for nest survival at high values of canopy closure suggested that nest survival in areas of high canopy closure was highly variable (Fig. 3b). We measured canopy closure at the nest structure, not at distances from the substrate representative of stand-level conditions. Most nests were in snags that do not contribute foliage to measures of canopy closure. Large, old snags are often found in small forest openings (Clinton et al. 1993, Hunter and Parker 1993), presumably because they excluded competition while alive. The opening created when a dominant tree dies and begins to decay persists until forest succession begins filling the gap, creating a window of time when the site is suitable for nesting by Brown Creepers. By the time forest succession fills the canopy gap, this window appears to close because of the sloughing of bark from the snag and the gradual loss of microsites suitable for a nest.

#### RECOMMENDATIONS

Our results confirm the need to consider both fine-scale local habitat and surrounding habitats when managing for species and populations. At the local scale, our results suggest that managing for the recruitment of large trees and retaining

large snags will benefit Brown Creepers. Large trees and snags are less abundant than they were historically and are beneficial to a wide variety of wildlife species (e.g., Verner et al. 1992, Noss et al. 2006, Purcell 2007, Bagne et al. 2008, Purcell et al. 2009).

At the landscape scale, Brown Creepers responded to edges negatively, particularly those with greater contrast between adjacent patches that primarily resulted from natural discontinuities. Questions related to edge sensitivity in areas where the mosaic of landscape patterns has resulted from natural phenomena such as topographical relief and disturbances such as fire, wind, and disease deserve further study. New research should consider edges of different severities and compare natural and man-made edges. Because differences in habitat qualities of adjacent patches are predicted to influence the strength of edge responses (Ries and Sisk 2004), we suggest that it may be profitable to investigate edge responses in terms of differences in factors related to habitat quality rather than simply in terms of differences in vegetation structure and composition.

## ACKNOWLEDGMENTS

We thank the many field biologists who helped collect data over the eight years of the study: L. Alamo, D. Artimez, A. Ayala, K. Bagne, H. Beeler, R. Brogle, K. Bush, C. Campbell, J. Campbell, C. Caris, C. Caurant, J. Cezniak, D. Cubanski, S. Deal, K. DeGroot, S. Ebrahim, B. Gibson, J. Hartwig, J. Jacobson, E. Keenan, R. King, A. Lense, J. Lindsey, J. Lower, K. Mazzocco, R. Miller, S. Morales, L. Nason, D. Nelson, B. Nielsen, J. Ohanesian, R. Olsen, M. Ossanna, R. Ryan, C. Seck, M. Seeley, N. Sherman, D. Smith, C. Snow, S. Sutton-Mazzocco, R. Swanerg, E. Talamantez, A. Tenneboe, K. Thumlert, J. Turner, M. Verner, K. Weeks, M. Westehuebe, V. Wible, R. Wilson, and R. Young. This project was funded by the U.S. Forest Service, Pacific Southwest Research Station. We thank the Sierra National Forest for logistical help and GIS data. Statistical advice and review were provided by Sylvia Mori and Jim Baldwin. The manuscript benefited by reviews from Karen Bagne and two reviewing editors.

## LITERATURE CITED

- ANDRÉN, H. 1995. Effects of landscape composition of predation rates at habitat edges, p. 225–255. *In* L. Hansson, F. Hahrif, and G. Merriam [EDS.], *Mosaic landscapes and ecological processes*. Chapman and Hall, London.
- ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175–1178.
- BAGNE, K. E. 2006. The effects of prescribed burning in the spring on avian communities in the Sierra Nevada of California. Ph.D. dissertation, University of California, Riverside, CA.
- BAGNE, K. E., K. L. PURCELL, AND J. T. ROTENBERRY. 2008. Prescribed fire, snag population dynamics, and avian nest site selection. *Forest Ecology and Management* 255:99–105.
- BEDDY, E. C. 1981. Bird communities and forest structure in the Sierra Nevada of California. *Condor* 83:97–105.
- BEYER, H. L. [ONLINE]. 2004. Hawth's analysis tools for ArcGIS. <<http://www.spatialecology.com/htools>> (31 August 2011).
- BOYCE, M. S. 1979. Seasonality and patterns of natural selection for life histories. *American Naturalist* 114:569–583.
- BRAND, L. A. 2004. Prediction and assessment of edge response and abundance for desert riparian birds in southeastern Arizona. Ph.D. dissertation, Colorado State University, Fort Collins, CO.
- BRAND, L. A., AND T. L. GEORGE. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. *Auk* 118:678–686.
- BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2<sup>nd</sup> edition. Springer-Verlag, New York.
- CALPIF (CALIFORNIA PARTNERS IN FLIGHT). 2002. Version 1.0. The draft coniferous forest bird conservation plan: a strategy for protecting and managing coniferous forest habitats and associated birds in California (J. Robinson and J. Alexander, lead authors). Point Reyes Bird Observatory, Stinson Beach, CA. <<http://www.prbo.org/calpif/plans.html>> (31 August 2011).
- CLINTON, B. D., L. R. BORING, AND W. T. SWANK. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology* 75:1551–1558.
- DAVIS, C. M. 1978. A nesting study of the Brown Creeper. *Living Bird* 17:237–263.
- DONOVAN, T. M., P. W. JONES, E. M. ANNAN, AND F. R. THOMPSON. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075.
- DUGUAY, J. P., P. B. WOOD, AND G. W. MILLER. 2000. Effects of timber harvests on invertebrate biomass and avian nest success. *Wildlife Society Bulletin* 28:1123–1131.
- FLETCHER, R. J. JR., L. RIES, J. BATTIN, AND A. D. CHALFOUN. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Canadian Journal of Zoology* 85:1017–1030.
- FREEMARK, K. E., AND B. COLLINS. 1992. Landscape ecology of birds breeding in temperate forest fragments, p. 443–454. *In* J. M. Hagan III, and D. W. Johnston [EDS.], *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- FRIEDMANN, H., AND L. F. KIFF. 1985. The parasitic cowbirds and their hosts. *Proceedings of the Western Foundation of Vertebrate Zoology* 2:226–304.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- GEORGE, T. L., AND D. S. DOBKIN. 2002. Introduction: habitat fragmentation and western birds. *Studies in Avian Biology* 25:4–7.
- GRANT, T. A., T. L. SHAFFER, E. M. MADDEN, AND P. J. PIETZ. 2005. Time-specific variation in passerine nest survival: new insights into old questions. *Auk* 122:661–72.
- HALL, L. S., P. R. KRAUSMAN, AND M. L. MORRISON. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:173–182.
- HAWROT, R. Y., AND G. J. NIEMI. 1996. Effects of edge type and patch shape on avian communities in a mixed conifer-hardwood forest. *Auk* 113:586–598.
- HEJL, S. J., D. EVANS MACK, J. S. YOUNG, J. C. BEDNARZ, AND R. L. HUTTO. 2002b. Birds and changing landscape patterns in conifer forests of the north-central Rocky Mountains. *Studies in Avian Biology* 25:113–129.
- HEJL, S. J., K. R. NEWLON, M. E. MCFADZEN, J. S. YOUNG, AND C. K. GHALAMBOR. 2002a. Brown Creeper (*Certhia americana*), no 669. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- HEJL, S. J., AND J. VERNER. 1988. Evaluating avian-habitat relationships in red fir forests of the Sierra Nevada. *Transactions of the Western Section of the Wildlife Society* 24:121–34.
- HELLE, P., AND J. MUONA. 1985. Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. *Silva Fennica* 19:281–294.
- HUNTER, J. C., AND V. T. PARKER. 1993. The disturbance regime of an old-growth forest in coastal California. *Journal of Vegetation Science* 4:19–24.

- JOHNSTON, V. R. 1947. Breeding birds of the forest edge in Illinois. *Condor* 49:45–53.
- JOKIMÄKI, J., E. HUHTA, J. ITÄMIES, AND P. RAHKO. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Canadian Journal of Forest Research* 28:1068–1072.
- KRISTAN, W. B. III, A. J. LYNAM, M. W. PRICE, AND J. T. ROTENBERRY. 2003. Alternative causes of edge–abundance relationships in birds and small mammals of California coastal sage scrub. *Ecography* 26:29–44.
- KUITUNEN, M., AND P. HELLE. 1988. Relationship of the Common Treecreeper *Certhia familiaris* to edge effect and forest fragmentation. *Ornis Fennica* 65:150–5.
- KUMAR, S., T. J. STOHLGREN, AND G. W. CHONG. 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87:3186–3199.
- LAHTI, D. C. 2001. The “edge effect on nest predation” hypothesis after twenty years. *Biological Conservation* 99:365–374.
- LAY, D. W. 1938. How valuable are woodland clearings to birdlife? *Wilson Bulletin* 50:254–256.
- LEOPOLD, A. 1933. Game management. Charles Scribner's Sons, New York.
- MAYRHOFER, M. 2006. Spatial point processes and Brown Creepers (*Certhia americana*): estimating habitat use of a silvicultural experiment. M.Sc. thesis, University of Washington, Seattle, WA.
- MCGARIGAL, K., AND B. J. MARKS. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW-GTR-351.
- MCGARIGAL, K., AND W. C. MCCOMB. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65:235–260.
- MCKELVEY, K. S., AND J. D. JOHNSTON. 1992. Historical perspectives on the forests of the Sierra Nevada and the Transverse Ranges in southern California: forest conditions at the turn of the century, p. 225–246. *In* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck [TECH. COORDS.], *The California Spotted Owl: a technical assessment of its current status*. USDA Forest Service General Technical Report PSW-GTR-133.
- NELSON, S. K. 1988. Habitat use and densities of cavity nesting birds in the Oregon Coast Ranges. M.Sc. thesis, Oregon State University, Corvallis, OR.
- NOSS, R. F., AND A. COOPERRIDER. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Covelo, CA.
- NOSS, R. F., J. F. FRANKLIN, W. L. BAKER, T. SCHOENAGLE, AND P. B. MOYLE. 2006. Managing fire-prone forests in the western United States. *Frontiers in Ecology* 4:481–487.
- PATON, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8:17–26.
- PENHOLLOW, M. E., AND D. F. STAUFFER. 2000. Large-scale habitat relationships of neotropical migratory birds in Virginia. *Journal of Wildlife Management* 64:362–373.
- PURCELL, K. L. 1997. Use of a fiberscope for examining cavity nests. *Journal of Field Ornithology* 68:283–286.
- PURCELL, K. L. 2007. Nesting habitat of Warbling Vireos across an elevational gradient in the southern Sierra Nevada. *Journal of Field Ornithology* 78:230–240.
- PURCELL, K. L., A. K. MAZZONI, S. R. MORI, AND B. B. BOROSKI. 2009. Resting structures and resting habitat of fishers in the southern Sierra Nevada, California. *Forest Ecology and Management* 258:2696–2706.
- RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monographs* 86:1–66.
- RIES, L., R. J. FLETCHER JR., J. BATTIN, AND T. D. SISK. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35:491–522.
- RIES, L., AND T. D. SISK. 2004. A predictive model of edge effects. *Ecology* 85:2917–2926.
- RIES, L., AND T. D. SISK. 2010. What is an edge species? The implications of sensitivity to habitat edges. *Oikos* 119:1636–1642.
- ROSENBERG, K. V., J. D. LOWE, AND A. A. DHONDT. 1999. Effects of forest fragmentation on breeding tanagers: a continental perspective. *Conservation Biology* 13:568–583.
- ROSENBERG, K. V., AND M. G. RAPHAEL. 1986. Effects of forest fragmentation on vertebrates in douglas-fir forests, p. 263–272. *In* J. Verner, M. L. Morrison, C. J. Ralph [EDS.], *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, WI.
- SAS INSTITUTE. 2002. SAS procedures guide, version 8, vols. 1 and 2, release 9.2. SAS Institute, Inc., Cary, NC.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- SISK, T. D., AND J. BATTIN. 2002. Habitat edges and avian ecology: geographic patterns and insights for western landscapes. *Studies in Avian Biology* 25:30–48.
- STRAYER, D. L., M. E. POWER, W. F. FAGAN, S. T. A. PICKETT, AND J. BELNAP. 2003. A classification of ecological boundaries. *BioScience* 53:723–729.
- STURDIVANT, R. X., J. J. ROTELLA, AND R. E. RUSSELL. 2007. A smoothed residual based goodness-of-fit statistic for nest-survival models. *Studies in Avian Biology* 34:45–54.
- SUORSA, P., E. HUHTA, A. JÄNTTI, A. NIKULA, H. HELLE, M. KUITUNEN, V. KOIVUNEN, AND H. HAKKARAINEN. 2005. Thresholds in selection of breeding habitat by the Eurasian Treecreeper (*Certhia familiaris*). *Biological Conservation* 121:443–452.
- SUORSA, P., E. HUHTA, A. NIKULA, M. NIKINMAA, A. JÄNTTI, H. HELLE, H. HAKKARAINEN. 2003. Forest management is associated with physiological stress in an old-growth forest passerine. *Proceedings of the Royal Society of London B* 270:963–969.
- TEMPLE, S. A., AND J. R. CARY. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2:340–347.
- TEWKSBURY, J. J., S. J. HEJL, AND T. E. MARTIN. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890–2903.
- VERNER, J., AND A. S. BOSS. 1980. California wildlife and their habitats: western Sierra Nevada. USDA Forest Service General Technical Report PSW-GTR-37.
- VERNER, J., K. MCKELVEY, B. R. NOON, R. J. GUTIÉRREZ, G. I. GOULD JR., AND T. W. BECK. 1992. The California Spotted Owl: a technical assessment of its current status. USDA Forest Service General Technical Report PSW-GTR-133.
- VILLARD, M.-A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *Auk* 115:801–805.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forests, p. 125–205. *In* R. L. Burgess and D. M. Sharp [EDS.], *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- WILCOVE, D. S., C. H. McLELLAN, AND A. P. DOBSON. 1986. Habitat fragmentation in the temperate zone, p. 237–256. *In* M. E. Soulé [ED.], *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, MA.
- WILKIN, T. E., D. GARANT, A. G. GOSLER, AND B. C. SHELDON. 2007. Edge effects in the Great Tit: analyses of long-term data with GIS techniques. *Conservation Biology* 21:1207–1217.

APPENDIX. Categories of tree size and canopy closure, and ratings of suitability of habitat for reproduction of the Brown Creeper (*Certhia americana*) for tree-dominated habitats in the Sierra Nevada, as defined by California Wildlife Habitat Relationships (CWHR). All other habitats and categories were considered unsuitable. Each tree-size and canopy-closure rating, combined with the habitat types (e.g., ponderosa pine), defines a specific CWHR habitat classification. On the basis of available literature and scientific opinion, each habitat classification is assigned a habitat-suitability rating for reproduction, cover, and feeding. Only ratings for reproduction are shown here. For more details see <http://www.dfg.ca.gov/biogeodata/cwhr/>.

CWHR category	Size class	DBH
1	Seedling	<2.5 cm
2	Sapling	2.5–15.2 cm
3	Pole	15.2–27.9 cm
4	Small tree	27.9–61 cm
5	Medium/large tree	>61 cm
6	Multi-layered tree	Size class 5 trees over a distinct layer of size class 4 or 3 trees, total tree canopy exceeds 60% closure.

CWHR category	Closure class	Canopy closure
S	Sparse	10–24%
P	Open	25–39%
M	Moderate	40–59%
D	Dense	60–100%

Habitat type	Habitat-suitability rating		
	Low	Medium	High
Ponderosa pine	4P, 5P	3M, 3D	4M, 4D, 5M, 5D
Mixed conifer	3M, 3D, 4S, 4P, 5S	5P	4M, 4D, 5M, 5D, 6
Jeffrey pine	3M, 3D	4M, 4D	5M, 5D
White fir	3M, 3D		4M, 4D, 5D, 6
Red fir	3M, 3D, 4S, 4P, 5S	4M, 4D, 5P	5M, 5D
Montane hardwood–conifer	3P, 3M, 3D, 4P, 5P	4M, 4D	5M, 5D, 6
Montane riparian	4M, 4D	5M, 5D, 6	
Lodgepole pine	3P, 3M, 3D	4M, 4D, 5M, 5D	