RESPONSE OF PASSERINE BIRDS TO FOREST EDGE IN COAST REDWOOD FOREST FRAGMENTS

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ABSTRACT.—The response of passerine birds to forest edge was examined in old-growth and mature second-growth coast redwood (*Sequoia sempivirens*) forest in northern California. The study objectives were to determine which common passerine species are sensitive to edges during the breeding season and to estimate edge width for forest interior species. Response to edge was measured along twelve 100 × 400 m plots extending from the edge into the forest interior to obtain relative density of birds. Plots were surveyed 4 to 5 times in 1996 and 8 to10 times in 1997. We found that 14 common passerines showed a gradient of edge sensitivity. Steller's Jay (*Cyanocitta stelleri*) and Swainson's Thrush (*Catharus ustulatus*) had higher relative densities near edges than in the forest interior (*P* < 0.05) and were categorized as edge species. Brown Creeper (*Certhia americana*), Winter Wren (*Troglodytes troglodytes*), Pacific-slope Flycatcher (*Empidonax difficilis*), and Varied Thrush (*Ixoreus naevius*) had lower relative densities near edges (*P* < 0.05) and were categorized as interior birds. Based on exponential regression models, estimated edge widths were 140 m for Varied Thrushes, 85 m for Brown Creepers, 120 m for Winter Wrens, and 125 m for Pacific-slope Flycatchers. Creation of edges would probably benefit Steller's Jays (which may be a nest predator), may not benefit Swainson's Thrushes, and may be detrimental to species that avoid edges. We recommend that edge effects be taken into consideration when planning for the conservation of bird species in the region. *Received 18 January 2000, accepted 23 January 2001.*

HABITAT FRAGMENTATION affects the landscape by reducing the amount and proximity of remnant patches of suitable habitat and increasing the amount of edge. Avian species may respond to one or a combination of these changes in the landscape as a result of different biological mechanisms. However, when addressing the effects of habitat fragmentation, the concepts of forest-interior species and area-sensitive species have often been used interchangeably (Villard 1998). Sensitivity to habitat fragmentation generally has been studied by examining the response of a species to forest fragment area rather than distance from the forest edge (Forman et al. 1976, Whitcomb et al. 1981, Blake and Karr 1987, Robinson et al. 1995). It has often been assumed that a bird species is a forest-interior species if it is less abundant or absent from small forest patches. That approach confounds the effect of edge and patch size. For example, a species may require a minimum patch size of 10 ha due to large home range requirements, but might use all 10

ha (including edges) uniformly. Only a few studies have defined forest edge versus interior bird species by specifically examining edge avoidance (Kroodsma 1984, King et al. 1997, Germaine et al. 1997).

Species that require forest interior may avoid edges due to altered microclimate, vegetation structure, or high density of predators or brood parasites near edges (Temple 1986, Murcia 1995). Once a species has been found to be sensitive to edges, it is important for management purposes to know the distance into the forest interior that the effect of edge (called *edge width*) is observed (Wilcove et al. 1986). A number of authors have developed patch-area models based on edge width. Temple (1986) developed the core-area model illustrating the importance of calculating the interior forest area instead of total patch area, but he did not estimate the edge width empirically. Laurance and Yensen (1991) developed a method of estimating the total area of forest interior that is dependent on an empirical measurement of edge width but also did not provide an empirical measurement of the distance. Sisk and Margules (1993) developed the effective-area model that goes the next step of calculating the effective area based on measurements of bird

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density across edges. However, other than Sisk and Margules' (1993) calculation of bird density across edges, and Gates and Mosher's (1981) estimation of edge use by birds on the basis of dispersion of nests, no other studies have empirically estimated edge width based on actual use of edges by birds.

Most studies pertaining to the effect of habitat fragmentation on songbirds have focused on the eastern and central United States (Ambuel and Temple 1983, Lynch and Whigham 1984, Askins et al. 1989, Robbins et al. 1989). In the only study of its kind in the Douglas-fir (*Pseudotsuga mensiesii*) forests of the Pacific northwest, Rosenberg and Raphael (1986) found that few bird species showed sensitivity to patch size, although 12 passerine species showed avoidance of edges. Coast redwood (*Sequoia sempivirens*) forests have likewise undergone drastic fragmentation. Initial studies have shown that nest predation increases near redwood forest edges (Brand and George 2000) and that the Varied Thrush (*Ixoreus naevius*) is sensitive to patch size (Hurt 1996). However, there have been no studies designed to look at edge effects on avian community composition in coast redwood forests.

The primary purpose of this study was to identify which common passerine species inhabiting old-growth and mature second growth coast redwood forests are sensitive to edges during the breeding season. This may be important both for forest interior species that avoid edges because the edge habitat may be unsuitable, as well as for species that prefer edges and thus may be suffering higher rates of predation. The second objective was to estimate the edge width for forest-interior species as a tool to develop management recommendations.

METHODS

This study was conducted in redwood forest patches in Humboldt County, California, from May to August 1996 and 1997. Study sites were located on public lands managed by Humboldt Redwoods State Park, Redwood National Park, Prairie Creek Redwoods State Park, and the Arcata Community Forest. Study sites consisted of old-growth and mature second-growth (>80 years) coast redwood forest. The overstory of all stands was dominated by redwoods (>50%), but other species found in those stands included Douglas-fir, Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), red alder (*Al-*

nus rubra), California bay (*Umbellularia californica*), big-leaf maple (*Acer macrophyllum*), and tan-oak (*Lithocarpus densiflorus*). The understory was dominated by rhododendron (*Rhododendron macrophyllum*), salal (*Gaultheria shallon*), California huckleberry (*Vaccinium ovatum*), red huckleberry (*V. parviflorum*), cascara (*Rhamnus purshiana*), salmonberry (*Rubus spectabilis*), California blackberry (*R. ursinus*), Himalayan blackberry (*R. discolor*), and red elderberry (*Sambucus racemosa*).

The redwood region is characterized by a maritime climate with cool, dry summers (13 to 18°C) and wet, mild winters (7 to 13°C) (Harris 1991). Approximately 90% of the precipitation falls from October through April. Average annual rainfall ranges from 96 cm in Eureka to 177 cm near Orick.

In California, coast-redwood forests originally occurred as a wide strip on the west slope of the coast range. Only ~3.5% of the presettlement distribution remains as original growth (Larsen 1991). Much of the current distribution of old-growth and mature second-growth coast-redwood forest habitat is fragmented and bordered by natural as well as anthropogenically induced edges (Fox 1997).

We defined forest edge by gaps ≥100 m in the forest canopy occurring adjacent to continuous forest patches. Only abrupt edges were used in the study design consisting of a number of different types. Natural edges resulted from flood plains and prairies, and anthropogenically induced edges resulted from one power-line corridor, as well as residential development and roads. Accessible forest edge lengths of 0.5 to 4 km were identified from U.S. Geological Survey orthophotoquad maps and field reconnaissance. Acceptable study-site characteristics included a continuous gap in the forest canopy >100 m exterior to an adjacent forest, a sufficient interior forest area (>5 ha), and a location >1 km from other edge lengths. Study sites were within approximately three hours combined driving and hiking time from Arcata, California. Once an edge length was identified and measured with a map wheel, the location of the center for each plot was selected randomly. A distance of at least 1 km between plots is several times larger than the territory diameter of any of the bird species that were examined.

Twelve 4 ha rectangular plots were established. Plots were 100 m wide and extended 400 m into the forest perpendicular to the forest edge. Plots were surveyed within 2 h of sunrise by walking up one transect and down a parallel transect located 25 m on either side of the central plot line and stopping for 5 min at 50 m intervals (18 locations per plot). The location of each bird seen or heard was recorded as x,y-coordinates. Plots were surveyed 4 to 5 times in 1996 by two observers, and 8 to 10 times in 1997 by three observers. Observer visits were rotated sequentially so that each plot was visited approximately the same number of times by each observer.

For the analysis, plots were divided into sixteen 25 × 100 m distance intervals (bands) from the edge to interior. The response variable for each species was the number of detections within each band per plot per year (n = 16 bands × 12 plots × 2 years = 384). The total number of detections for a given species in each band-plot combination was converted from the x,y-coordinates of recorded bird locations. Because of short distances between transects and stops, individual birds may have been recorded more than once. As such, point recordings can not all be considered independent and that was taken into account in the analysis methodology in two ways. First, point recordings at each visit were summarized by band within each plot, and it was assumed that average counts per band were directly proportional to species-specific population density and that the proportionality factor is independent of distance from the edge within each field season. Consequently, ratios of average counts can be considered estimates of relative bird density (see Appendix). Second, possible multiple sightings of a specific bird at a particular visit could also occur across band boundaries. This and other forms of spatial autocorrelation would induce local dependence between relative density for adjacent or nearby bands. This band-to-band dependence was taken into account by use of a dispersion parameter and robust estimation of standard errors (see Appendix). The distance from edge was taken as the midpoint of the bands (12.5, 37.5, etc.) and treated as a continuous variable. Year was treated as an indicator variable (1996 or 1997).

An augmented form of Poisson regression was used, implemented by Generalized Estimating Equations (GEE) methods, to examine whether distance from the forest edge and the type of edge were affecting relative density of passerines (McCullagh and Nelder 1989, Liang and Zeger 1986). The Appendix includes a detailed description of the model used. To account for differences in the number of counting times, the number of visits per plot per year was log transformed and included in the model as an offset (McCullagh and Nelder 1989, see Appendix). Additionally, three strategies were employed to augment the Poisson regression approach. First, to account for inherent differences in bird density from plot to plot, random plot effects were included in the augmented Poisson regression model. Second, a scale parameter was included in the model which, in effect, extends Poisson regression to allow the variance to be greater than or less than the mean. That is, bird detections within bands were allowed to be under- or over-dispersed compared to a standard Poisson distribution. Non-Poisson dispersion of count data could result from aggregation of birds within territories, repulsion of birds between territories, possible failure to detect individual birds, or multiple detections of individual birds. Finally, the Hubur/White/sandwich estimator, as implemented

in GEE, was used to obtain robust estimates of standard errors. This is a theory developed to give consistent P-values and correct inferential results even when the analysis model is incorrectly specified (Liang and Zeger 1986). This analysis was done for the 14 most common passerines (those species with >60 detections over the two field seasons). The analyses of relative bird density was done with the "xtgee" command in Stata 5.0 statistical analysis software (StataCorp 1997).

Yahner (1988) suggested that the "functional use of edges by wildlife" be used to quantify edge effects, although he did not recommend a specific method for doing so. In this study, edge width was operationally defined for edge sensitive species on the basis of an exponential regression model with one asymptote. First, the species sensitive to edges were identified. Interior species were defined as those having significantly lower relative density along the edge than in the forest interior. The interior species were first modeled by a "saturated" model, implemented by GEE, which provides an estimate of the mean observed bird counts in each band adjusted for the other covariates in the model. The band-specific mean observed bird counts were converted to relative density (see Appendix) then smoothed by an exponential function ($Y=b_1(1-b_2{}^x)$) with one asymptote and two parameters (b_1 and b_2) where x = distance from edge. It was necessary to use the average relative density per band to estimate the exponential regression model because the GEE methodology has not yet been developed to work with count data for exponential models. *Edge width* was defined as the distance from the edge at which 90% of the asymptotic relative density is achieved.

Edge species were defined as those having significantly higher relative density along the edge band than in the forest interior. The relative density of edge species was graphed first with the saturated model, and then with an exponential function with one asymptote. The edge width was not determined for the edge species.

RESULTS

Passerine species of the coast redwoods included in this analysis showed different patterns of relative density in relation to distance from the forest edge. Of the 14 most-common species, most observations were of Pacific-slope Flycatcher (1767 observations) and Winter Wren (1242 observations), whereas Red-breasted Nuthatch (85 observations) and American Robin (74 observations) were observed the least.

Steller's Jay and Swainson's Thrush were categorized as edge species with approximately

TABLE 1.   Relative density of common passerines in relation to distance from the forest edge in coast red-wood forests of northern California. The average count per band = exp[ln(number of visits) + B_0 + B_1 (distance) + B_2 (year)][a]. A negative coefficient indicates decreased relative density with distance, and a positive coefficient indicates increased relative density with distance.

Species		Coef. (B_1)	Robust S.E.	P-value	Relative Density[b]		
					0 m	200 m	400 m
Pacific-slope Flycatcher	*Empidonax difficilis*	0.0011	0.0003	0.001	1.00	1.26	1.58
Steller's Jay	*Cyanocitta stelleri*	−0.0018	0.0007	0.008	1.00	0.69	0.48
Common Raven	*Corvus corax*	−0.0001	0.0017	0.931	1.00	0.97	0.94
Chestnut-backed Chickadee	*Parus rufescens*	−0.0001	0.0006	0.886	1.00	0.98	0.97
Red-breasted Nuthatch	*Sitta canadensis*	0.0024	0.0012	0.052	1.00	1.63	2.64
Brown Creeper	*Certhia americana*	0.0015	0.0005	0.003	1.00	1.36	1.84
Winter Wren	*Troglodytes troglodytes*	0.0016	0.0006	0.004	1.00	1.38	1.91
Golden-crowned Kinglet	*Regulus satrapa*	0.0002	0.0006	0.703	1.00	1.05	1.10
Swainson's Thrush	*Catharus ustulatus*	−0.0017	0.0008	0.030	1.00	0.71	0.51
American Robin	*Turdus migratorius*	−0.0022	0.0018	0.216	1.00	0.64	0.42
Varied Thrush	*Ixoreus naevius*	0.0019	0.0005	0.000	1.00	1.47	2.18
Wrentit	*Chamaea fasciata*	0.0014	0.0025	0.571	1.00	1.32	1.74
Hermit Warbler	*Dendroica occidentalis*	0.0014	0.0009	0.128	1.00	1.31	1.72
Wilson's Warbler	*Wilsonia pusilla*	0.0002	0.0004	0.582	1.00	1.05	1.10

[a] See appendix for a detailed description of the augmented Poisson regression model.

[b] The relative density of each species at 0, 200, and 400 m from the edge was obtained by taking the value of *e* raised to the coefficient multiplied by the distance from edge. For example, the relative density for the Varied Thrush at 400 m from the edge = exp[0.0019(400)] = 2.14 times the relative density at the edge. (The slight discrepancy is due to rounding of coefficients in this table). Please see appendix for a description of the general method of interpreting Poisson regression model parameters.

half of their relative density at 400 m as at the forest edge (Table 1). American Robin showed a similar tendency but the relationship was not significant (P = 0.21). Five species appeared unaffected by distance from the forest edge (P ≥ 0.571) with a relative density at 400 m from the edge ranging from 0.94 to 1.74 times the relative density at the forest edge (Common Raven, Chestnut-backed Chickadee, Golden-crowned Kinglet, Wrentit, and Wilson's Warbler). Hermit Warbler and Red-breasted Nuthatch showed nonsignificant (P ≤ 0.128) although substantial tendencies for lower relative density close to the forest edge, with a relative density at 400 m from the edge ranging from 1.72 to 2.64× that at the forest edge. Four species were categorized as forest interior birds: Brown Creeper, Winter Wren, Pacific-slope Flycatcher, and Varied Thrush with a relative density at 400 m from the edge ranging from 1.58 to 2.18× the relative density at the forest edge (Table 1).

Relative density was plotted for the six species that showed a significant effect of distance from the forest edge. For the forest-interior species, there were very few detections of birds from 0 to 25 m from the edge. Detections increased from 25 to 100 m from the edge, and then a leveled off from approximately 100 to 400 m. Based on exponential model smoothing

of the relative density per band, the estimated edge width was 140 m for the Varied Thrush, 85 m for the Brown Creeper, 120 m for the Winter Wren, and 125 m for the Pacific-slope Flycatcher (Fig. 1). The relative density of the two edge species decreased in relation to distance from the forest edge (Fig. 2).

DISCUSSION

Estimating edge sensitivity is one method of identifying species that may be affected by forest fragmentation. Biotic and abiotic differences between edges and forest-interior locations, such as differences in predation (Gates and Gysel 1978), microclimate (Chen et al. 1993), vegetation structure (Ranney et al. 1981), and insect composition (Shure and Phillips 1991), probably affect different species in different ways depending on their breeding and foraging requirements. Patch size has often been used to measure sensitivity to forest fragmentation. Although patch-size sensitivity and edge sensitivity are probably correlated (due to edge influences that operate on a larger proportion of the area in smaller patches than in larger patches), patch size is not a precise measure of edge sensitivity nor vice versa (Villard 1998).
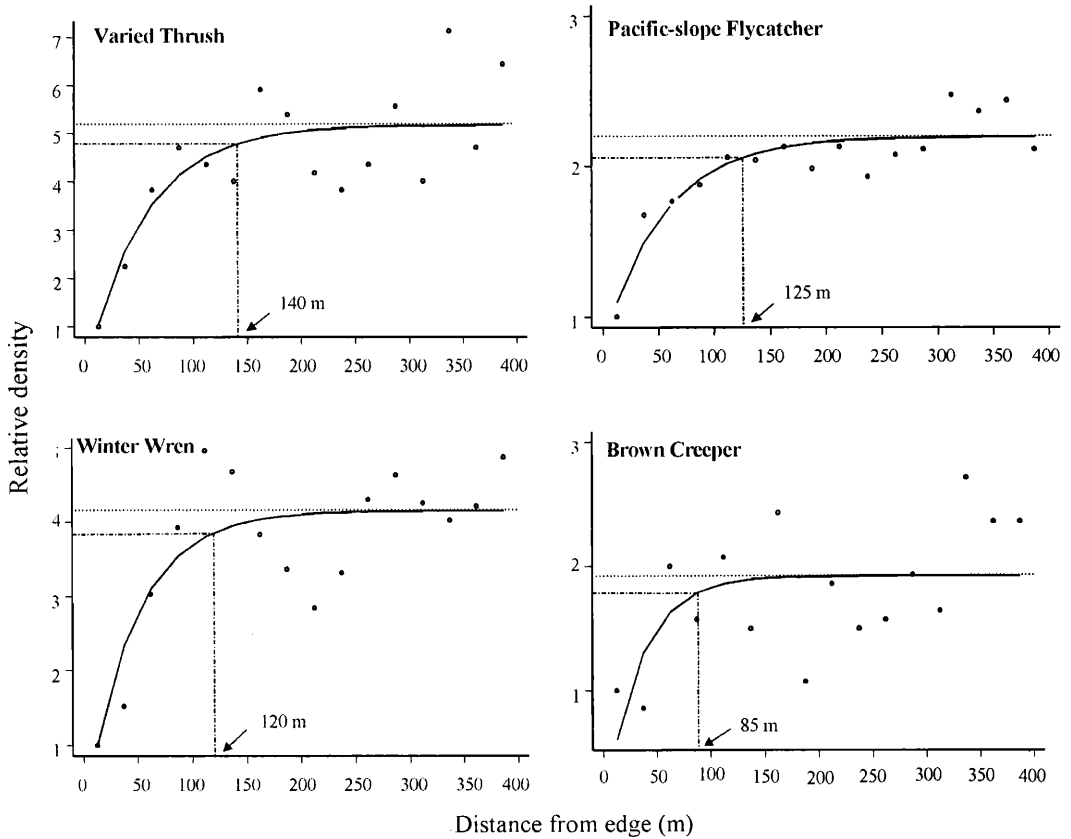
FIG. 1. Relative density with respect to distance from the forest edge and estimated edge width for the Varied Thrush, Pacific-slope Flycatcher, Winter Wren, and Brown Creeper. The points represent the band-specific relative density. The smooth curve represents the relative density based on an exponential regression model with one asymptote. The dotted line shows the asymptotic relative density and the dash–dot line illustrates the edge width defined as the distance from edge at which 90% of the asymptotic relative density has been achieved.

Edge-sensitive species.—The edge-sensitive species found in this study concurred relatively well with other studies that measured sensitivity to forest fragmentation. Winter Wrens have been found to be sensitive to edges (Rosenberg and Raphael 1986), patch size (Rosenberg and Raphael 1986), and clearcuts embedded in old-growth (Hejl and Paige 1994). Varied Thrush distribution was positively related to forest-fragment size in an earlier study in coast red-woods (Hurt 1996). Pacific-slope Flycatcher, Brown Creeper, Red-breasted Nuthatch, and Hermit Warbler were also found to be sensitive to edges by Rosenberg and Raphael (1986).

There are many possible explanations for edge sensitivity. Some species that avoided edges show habitat preference for moist for-

ests. Winter Wrens breed in moist coniferous forests and nest in dense brush especially along stream banks (Ehrlich et al. 1988). Barrows (1986) found that Winter Wrens in California had broad habitat preferences in fall and winter, but that habitat selection shifted in the breeding season almost exclusively to old-growth forest characterized by dense, moist understory. Likewise, McGarigal and McComb (1992) found that the Winter Wren was associated with riparian systems in Oregon. The Varied Thrush breeds in moist coniferous forest with a dense understory and is associated with streams (Beck 1997). The Pacific-slope Flycatcher breeds in forests especially near water (Ehrlich et al. 1988). Edges receive higher levels of incident radiation, and thus microclimate near
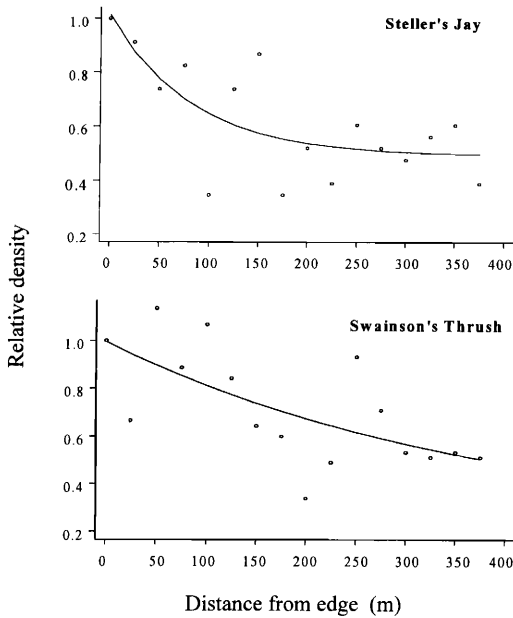
FIG. 2. Relative density with respect to distance from the forest edge for the Steller's Jay and Swainson's Thrush.

edges (such as temperature and humidity) required by those species may be altered. Microclimate changes, in turn, could affect vegetation composition and structure as well as the prey base near edges. It is also possible that the species that avoid edges may be responding to selection pressure of increased predation over ecological time.

Edge-neutral species.—The Chestnut-backed Chickadee, Golden-crowned Kinglet, Wrentit, Wilson's Warbler, and Common Raven showed no evidence for avoiding or preferring edges in coast redwoods. This contrasts with a study in Douglas-fir forests in which The Chestnut-backed Chickadee and Golden-crowned Kinglet were found to avoid edges (Rosenberg and Raphael 1986).

Edge-preferring species.—The American Robin was found to be an edge bird in the eastern United States (Johnston and Odum 1956). The American Robin also showed that tendency in this study, but small sample size probably resulted in inconclusive results. Steller's Jays had higher relative abundance near edges and were observed taking eggs out of artificial nests (L. A. Brand pers. obs.). In contrast to Steller's Jays, Swainson's Thrushes may be caught in an ecological trap (Gates and Gysel 1978, Ratti and

Reese 1988). Brand and George (2000) used artificial nests and found predation to be significantly higher near edges than in the forest interior in coast-redwood forest stands. If Swainson's Thrushes have higher relative density closer to edges because they are selecting edges for nesting, then they may also be suffering higher levels of nest predation near edges. Though edge-preferring species may also have mechanisms to reduce predation, it is questionable whether the active creation of edges would be beneficial for Swainson's Thrush, and that is an area which warrants further study.

The average edge width of the four forest-interior species is ~115 m. The distance of 115 m from the forest edge also corresponds with the distance at which the probability of predation on artificial nests declines by half (Brand and George 2000). An estimate of 115 m edge width and a 115 m diameter core area suggests that a circular forest patch should be a minimum of 9.3 ha in order to have 1 ha of interior habitat. However, this size may not be adequate depending on the territory size of a given species. The edge widths estimated in this study can be used to predict patch sizes that, in effect, would be all edge for particular forest interior species. For example, a 140 m edge width for Varied Thrushes suggests that a circular patch size of 6.2 ha consists of only edge habitat. However, Hurt (1996) found Varied Thrushes required a minimum patch size in coast-redwood forests of 16 ha, thus suggesting that a minimum of 2.3 ha of forest interior are required.

CONCLUSION

Recommendations for the common species that breed in the redwood forest region can be made from the results of this study. (1) The creation of edge would probably benefit Steller's Jays, but that species may be a nest predator and is not a bird of conservation concern. (2) It is questionable whether the active creation of edges would be benefit Swainson's Thrushes. Further study is needed to investigate whether Swainson's Thrushes are suffering higher rates of nest predation near edges in coast-redwood forest similar to that which has been found using artificial nests (Brand and George 2000). (3) Creation of edge may be detrimental to Pacific Slope Flycatcher, Varied Thrush, Winter Wren,

and Brown Creeper, as well as Red-breasted Nuthatch and Hermit Warbler.

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APPENDIX: Description of the model used for augmented poisson regression analysis. This study of relative bird density as a function of distance from the forest edge was based on the total observed bird counts per band per plot per year. For each band, the total observed bird count was the sum of the counts observed over all visits to the plot during each of two field seasons. The year was treated as a binary predictor variable that allowed for a systematic shift in average counts across all plot-band combinations. Because the number of visits varied somewhat from plot to plot, that varying amount of observation time had to be accounted for in the analysis model.

Let C_{pbv} represent the count observed in plot p in band b for visit v for a given bird species. As the preliminary step in modeling, those counts were assumed to be Poisson distributed observations with an average $\lambda_{pbv} > 0$ according to the probability model:

$$P(C_{pbv}) = \frac{e^{-\lambda_{pbv}} \lambda_{pbv}{}^{C_{pbv}}}{C_{pbv}!}; \quad \text{where } C_{pbv} = 0, 1, 2, \ldots$$

Across visits for a specific plot and band combination, the variability of counts around the mean are assumed to be independent. For example, bird activity levels, and thus the likelihood of detection, may vary around the average for a particular band due to weather conditions that can change from visit to visit within a single field season. From the additive property for independent Poisson counts, it therefore follows that the total count C_{pb} for the band over V_p total number of visits over both years is distributed according to the Poisson probability model:

$$P(C_{pb}) = \frac{e^{-V_p \lambda_{pb}} V_p \lambda_{pb}{}^{C_{pb}}}{C_{pb}!}; \quad \text{where } C_{pb} = 0, 1, 2, \ldots$$

with average count λ_{pb} = average of λ_{pbv} across V_p visits.

The basic Poisson model can be extended to the Poisson Regression Model (PRM) by letting:

$$\lambda_{pb} = \exp[B_0 + B_1(x_1) + B_2(x_2) + \cdots + B_L(x_L)]$$

such that

$$\ln(\lambda_{pb}) = B_0 + B_1(x_1) + B_2(x_2) + \cdots + B_L(x_L)$$

where $B_0, B_1, B_2, \ldots, B_L$ are the regression model coefficients to be fitted to the data and $x_1, x_2, \ldots, x_L$ are the predictors of the average total counts per band per plot. The exponential form is generally used because it forces the average count parameter λ_{pb} to be >0. Note that the natural log transformation will cause $\ln(\lambda_{pb})$ to be a linear model.

In the PRM the average total count for band b in plot p is:

$$\lambda_{pb} = V_p\exp[B_0 + B_1(x_1) + B_2(x_2) + \cdots + B_L(x_L)]$$

$$= \exp[\ln(V_p) + B_0 + B_1(x_1)$$

$$+ B_2(x_2) + \cdots + B_L(x_L)]$$

where the term $\ln(V_p)$ serves as a predictor with a known regression coefficient equal to one. A term of this type is called an offset (McCullagh and Nelder 1989). The offset allows the PRM to deal with varying numbers of visits and provides a way to study systematic differences in λ_{pb} depending on distance from the edge.

However, the PRM has two important limitations relative to the analysis requirement for this study. First, standard Poisson regression requires that the variance of observed counts equal the average of observed counts. This property seldom holds in biological applications (McCullagh and Nelder 1989) and is unlikely to be appropriate here. Secondly, the PRM requires that the total count outcomes for the different band and plot combinations be statistically independent. As discussed in the methods section, the count data, although independent from plot to plot, are not likely to be independent from band to band within a plot. Fortunately, both of the restrictive assumptions of the PRM can be relaxed.

The generalized linear model (GLM) (McCullagh and Nelder 1989, Nelder and Wedderburn 1972), which can be implemented by the Stata glm and xtgee commands (StataCorp 1997), allow the count variance to be proportional, rather than necessarily equal, to the average count. This is achieved with a proportionality (scale) parameter that can be higher than or less than 1 corresponding to over- or underdispersion relative to λ_{pb}. The scale parameter is estimated from the data. For this analysis, the scale(dev) option with xtgee was used, in which the scale parameter was set to the deviance divided by the residual degrees of freedom.

The PRM has been generalized further by the generalized estimating equation (GEE) extension of GLM (Liang and Zeger 1986, Liang 1987). GEE al-

lows for statistically dependent data from band to band within plots and also allows for plot to plot variation (Liang and Zeger 1986). The GEE method uses a "working correlation matrix" (Liang and Zeger 1986) to represent plot to plot variation and provide an approximate model for the correlation between counts from different bands in the same plot. For this analysis the "exchangeable" working correlation matrix was used. In addition, a "robust" method for estimating standard errors of regression coefficients and P-values is provided that accounts for the fact that the working correlation matrix used for the analysis may not fully agree with the true situation (Liang and Zeger 1986). The robust and correlation (exchangeable) options were used with the Stata xtgee command to do the analysis.

Interpretation of model coefficients.—With the bird counts obtained in this project, it is only reasonable to make the working assumption that the average of observed counts in a particular plot-band (25×100 m area) per year are proportional to the true average bird density in the corresponding plot-band area per year. Assuming that the proportionality factor relating the average of observed counts to underlying bird density is independent of distance from edge, it is possible to estimate the relative density (ratios of average bird counts) from the outermost (edge) band relative to bands at varying distances from the edge.

A general procedure for interpretation of PRM coefficients is based on ratios of average counts at two predictor points; $x_1^{[1]}, x_2^{[1]}, \ldots, x_L^{[1]}$ versus $x_1^{[2]}, x_2^{[2]}, \ldots, x_L^{[2]}$. Let $RD_{[1][2]}$ = relative density at predictor point [1] versus predictor point [2]. Then,

$$RD_{[1][2]} = \frac{\lambda_{pby} \text{ at } x_1^{[1]}, x_2^{[1]}, \ldots, x_L^{[1]}}{\lambda_{pby} \text{ at } x_1^{[2]}, x_2^{[2]}, \ldots, x_L^{[2]}}$$

$$= \langle\exp\{\ln(V_p) + B_0 + B_1(x_1^{[1]})$$

$$+ B_2(x_2^{[1]}) + \cdots + B_L(x_L^{[1]})\}\rangle$$

$$\div \langle\exp\{\ln(V_p) + B_0 + B_1(x_1^{[2]})$$

$$+ B_2(x_2^{[2]}) + \cdots + B_L(x_L^{[2]})\}\rangle$$

$$= \exp\{B_1(x_1^{[1]} - x_1^{[2]})$$

$$+ B_2(x_2^{[1]} - x_2^{[2]}) + \cdots$$

$$+ B_L(x_L^{[1]} - x_L^{[2]})\}$$

For example, if x_2 through x_L are the same at both predictor points and x_1 is a continuous predictor for the distance from edge coded $x_1^{[2]} = 0$ at the edge and $x_1^{[1]} = 1$ for 1 m away from the edge, then $\exp(B_1(\Delta d))$ is the ratio of relative density at Δd meters away from the edge versus the edge.