THE EFFECTS OF HABITAT FRAGMENTATION ON BIRDS IN COAST REDWOOD FORESTS

T. Luke George and L. Arriana Brand

Abstract. Human activities in the redwood (*Sequoia sempervirens*) region over the last 150 years have changed what was once a relatively continuous old-growth forest ecosystem into a highly fragmented mosaic of young, mature, and old-growth forest patches, agricultural land, and human settlements. We summarize recent studies on the effects of forest fragmentation on diurnal landbirds in redwood forests and present new analyses of the effects of forest patch size on the distribution and abundance of breeding birds. Analyses of the relative abundance of 31 bird species in 38 patches of mature and old-growth redwood forest indicate that six species were positively correlated with forest patch area and may be sensitive to fragmentation: Pileated Woodpecker (*Dryocopus pileatus*), Pacific-slope Flycatcher (*Empidonax difficilis*), Steller's Jay (*Cyanocitta stelleri*), Brown Creeper (*Certhis americana*), Winter Wren (*Troglodytes troglodytes*), and Varied Thrush (*Ixoreus naevius*). These species (except the Steller's Jay) have been identified as sensitive to forest fragmentation in other studies of wet coniferous forests in the western U.S. The American Robin (*Turdus migratorius*), Orange-crowned Warbler (*Vermivora celata*), Dark-eyed Junco (*Junco hyemalis*), and Song Sparrow (*Melospiza melodia*) were negatively correlated with patch area. Song Sparrows and Orange-crowned Warblers are more abundant in young second-growth than mature redwood forests, and American Robins and Dark-eyed Juncos are generally associated with forest openings. Thus, these four species are associated with and likely responding to habitats surrounding forest patches. Previous analyses have shown that four of the species that were positively associated with patch area, Pacific-slope Flycatchers, Brown Creepers, Winter Wrens, and Varied Thrushes, were less abundant at forest edges than the forest interior, suggesting that edge avoidance may be responsible for their sensitivity to fragmentation. Two species, Steller's Jay and Swainson's Thrush (*Catharus ustulatus*), were more abundant along forest edges. In a previous study, we found that predation on artificial nests increased with proximity to forest edge and that Steller's Jays were observed preying on some of the nests. These and other studies suggest that several bird species are sensitive to fragmentation of old-growth and mature second-growth coast redwoods possibly due to changes in microclimate along forest edges or to increased nest predation and subsequent avoidance of forest edges. Implementation of forest practices that reduce the amount of forest edge on the landscape may reduce the potential impacts of fragmentation on bird species in redwood forests.

Key Words: area effects; artificial nests; diurnal landbirds; edge effects; forest fragmentation; nesting success; redwoods; *Sequoia sempervirens*.

Numerous studies have documented the negative effects of forest loss and fragmentation on birds breeding in forests of the midwestern and eastern United States (Ambuel and Temple 1982, Askins et al. 1990, Robinson and Wilcove 1994, Walters 1998, Thompson et al. *this volume*) and Europe (Andrén 1992, 1994). Furthermore, a consensus is emerging among scientists working in these regions that habitat fragmentation results in increased nest predation and parasitism, thereby reducing breeding productivity and possibly leading to population declines. Thompson et al. (*this volume*) have proposed a "top-down" hierarchical model that includes regional, landscape-level, and local effects to explain variation in nesting success across the landscape. However, there is substantial variation among studies and some results in western forests seem to contradict the general pattern (e.g., Tewksbury et al. 1998). This has led to suggestions that the "Eastern Paradigm" may not be applicable to western forests.

Over the last 150 years, Westside forests (for-ests west of the Sierra Nevada/Cascade crest) have been extensively logged, resulting in a fragmented pattern of late-seral stage forest in a sea of younger forest (Garmen et al. 1999). Because forest fragmentation has had such a dramatic impact on birds in other regions, it has been suggested that similar effects may be occurring in Westside forests. However, while some species such as the Northern Spotted Owl (*Strix occidentalis caurina*) and Marbled Murrelet (*Brachyramphus marmoratus*) show strong negative responses to forest fragmentation, studies of passerines and other small bird species in Westside forests have documented few effects of forest fragmentation (Rosenberg and Raphael 1986, Lehmkuhl et al. 1991, McGarigal and McComb 1995).

A number of hypotheses have been suggested to explain the lack of response of birds to forest fragmentation in Westside forests, including: (1) insufficient time for species to respond (Rosenberg and Raphael 1986, Lehmkuhl et al. 1991), (2) limited extent of forest loss (Rosenberg and

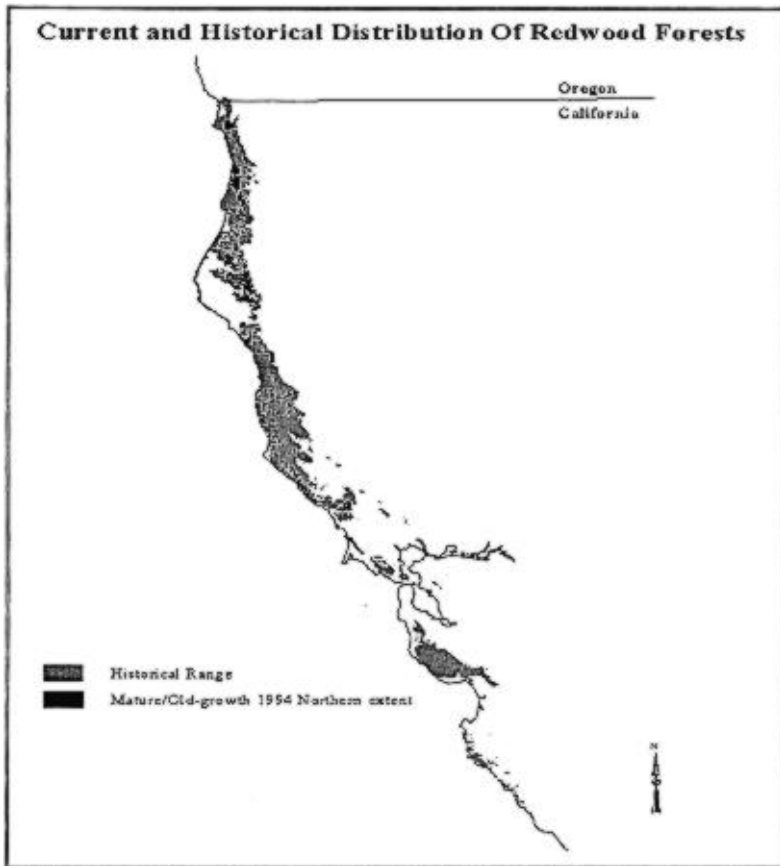**Current and Historical Distribution Of Redwood Forests**

FIGURE 1. Original distribution of coast redwood (*Sequoia sempervirens*) forests and current distribution of old-growth and mature second-growth coast redwood forest north of Point Reyes National Seashore. Current distributions are based on Landsat satellite imagery (Fox 1997).

Raphael 1986, Lehmkuhl et al. 1991), (3) the matrix (generally young forest) is less detrimental to nesting birds (McGarigal and McComb 1995), and (4) the species are adapted to heterogeneous landscapes and thus to the kinds of changes that logging has produced on the landscape (McGarigal and McComb 1995, Hejl et al. *this volume*). The first two hypotheses do not rule out fragmentation effects but suggest that effects may only be evident in forests that have been logged extensively in the past. The latter two hypotheses imply that forest fragmentation due to logging will have little effect even in heavily logged regions of the western United States.

Coast redwood (*Sequoia sempervirens*) forests have been heavily logged since the mid 1800s. Only about 3.5% of the pre-settlement distribution remains as original growth, and the current distribution of mature and old-growth redwood forest habitat is highly fragmented

(Fig. 1; Larsen 1991). Logging began earlier and has occurred more extensively in redwood than in other Westside forests (Sawyer et al. 2000). Thus, the effects of fragmentation may be more evident in redwood than in other Westside forests.

The birds of the redwood forest have not been extensively studied. However, over the past several years there have been a number of studies that have examined the effects of forest fragmentation on the birds of the region. Our objectives in this paper are to: (1) present new analyses of bird response to patch size and nesting success of Winter Wrens and Swainson's Thrushes (see Table 1 for scientific names of bird species studied) with respect to distance from forest edge, (2) summarize published and unpublished studies on the effects of forest fragmentation on birds in redwood forests, and (3) compare the effects of forest fragmentation on

birds in redwood forests to those found in the Midwest and the eastern United States.

METHODS

We describe the methods for the analysis of bird response to patch size and nesting success of Winter Wrens and Swainson's Thrushes in detail, as these analyses have not been published. Methods for estimates of relative bird abundance with respect to distance from forest edge and the artificial nest experiments have been published elsewhere (Brand 1998; Brand and George 2000, 2001).

STUDY AREA

We conducted our studies in redwood forest patches in Humboldt County, California. Point counts that we used for analysis of bird response to patch size were conducted from 1 May to 15 July, 1994. Monitoring of Winter Wren and Swainson's Thrush nests took place during May–August 1998–1999. Study sites consisted of old-growth as well as mature second-growth (>80 years) coast redwood forests. The overstory of all stands was dominated by redwoods (>50%), but other tree species found in these stands included Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), red alder (*Alnus rubra*), California bay (*Umbellularia californica*), big-leaf maple (*Acer macrophyllum*), and tan-oak (*Lithocarpus densiflorus*). The understory was dominated by rhododendron (*Rhododendron macrophyllum*), sword fern (*Polystichum munitum*), salal (*Gaultheria shallon*), California huckleberry (*Vaccinium ovatum*), red huckleberry (*Vaccinium parviflorum*), cascara (*Rhamnus purshiana*), salmonberry (*Rubus spectabilis*), California blackberry (*Rubus ursinus*), Himalayan blackberry (*Rubus discolor*), and red elderberry (*Sambucus racemosa*). The edge of each patch was defined by gaps ≥100 m in the forest canopy occurring adjacent to several features such as rivers, grasslands, young forest (<30 years), residential development, and roads.

Study sites were located on public lands managed by Humboldt Redwoods State Park, Redwood National Park, Prairie Creek Redwoods State Park, the City of Arcata (Arcata Community Forest), Humboldt State University Wildlife Department (Wright Wildlife Refuge), the City of Eureka (Sequoia Park), and Grizzly Creek State Park. Study sites were also located on Simpson Timber Company property and other private lands. Stands on privately owned land have been intensively managed in the past 100 years. Most of the sites on public lands have never been logged; some were logged once and are now mature stands (>100 years).

For the patch size study, we used orthophotographic quadrangles of the region to identify potential forest patches characterized by >50% redwood canopy and a stand age of >80 years. From approximately 90 eligible patches, we randomly chose 38 forest patches to survey. The size of patches ranged from 0.89 ha to 4252 ha. However, 35 of the 38 patches were <160 ha. The study sites were distributed over approximately 700 km², all within 50 km of the Pacific Ocean.

The fate of Winter Wren and Swainson's Thrush nests was studied at the Wright Wildlife Refuge, the Arcata Community Forest, and Redwood National Park. Plots were established along forest edge (edge plots) and in forest interior (interior plots, >400 m from forest edge). One edge plot was established at the Wright Wildlife Refuge, two interior and one edge plot were established in the Arcata Community Forest, and two interior plots were established in Redwood National Park. Both the Wright Wildlife Refuge and the Arcata Community forest bordered on suburban areas.

BIRD RESPONSE TO PATCH SIZE

To examine which passerine bird species are sensitive to forest patch size and shape during the avian breeding season, we investigated the distribution and relative abundance of birds in redwood forest patches using point counts (Verner 1985). The location of the first point in a patch was randomly selected. From that point, a direction was randomly chosen to establish the succeeding points placed 200 m apart, until no further points could be placed within the patch or we had established 4 points. Most points were >100 m from the edge of the patch. In some cases the size and shape of the patch made this impossible, but in all cases points were placed no closer than 50 m from the edge of the patch.

Each patch was surveyed four times (twice by each of two observers), approximately once every two weeks. Point counts lasted 8 min, and were conducted at least 5 min apart. Some patches were too small to contain four points. In these patches, we established fewer points but maintained equal sampling effort by conducting additional counts at the points. If one point was established in a patch, then four, 8-min point counts spaced 5 min apart were conducted at one point. If a patch contained two points, two point counts were conducted 5 min apart at each point. If a patch contained 3 points, two point counts were done at a randomly chosen point, then one point count was conducted at the two remaining points. If four points were established in a patch, one point count was conducted at each point. All point-counts were conducted within four hours after sunrise.

Data were recorded separately for each 8-min point count even if occurring 5 min apart in the same location. During an 8-min point count, birds were not counted twice unless there was a high certainty that it was a different individual of the same species. The number of birds counted at each point in each patch across all visits to each patch was summed to get an index of relative abundance for that patch.

To quantify the landscape variables of habitat patch size and patch shape, we used a planimeter and orthophotoquads to measure the area (ha) of each forest patch and a map wheel to measure the total perimeter (m) of each patch. Because perimeter length is correlated with area, we computed an index of patch shape using the ratio of the perimeter (m) of a given forest patch to the perimeter (m) of a circular forest patch of equal area. Both patch area and patch shape were log transformed for analysis.

Because the bird data are counts, we used Poisson regression (McCullagh and Nelder 1989) to examine the effect of patch area and shape on bird abundance. Only species that were observed in at least 20% of the patches were included in the analysis. We used the

natural log of patch area to deal with wide disparity in patch areas. The natural log of patch area and patch shape were correlated ($r^2 = 0.34$, df $= 36$, P $= 0.037$) and therefore we used only log patch area in the analyses because it explained a higher proportion of the variation in bird abundances than log patch shape, and patch area is generally a better predictor of bird abundance than patch shape (Galli et al. 1976, Blake and Karr 1987, Askins et al. 1990). A scale parameter was included in the model, which allows the variance to be greater than the mean to allow for over-dispersion of bird detections within patches compared to a standard Poisson distribution (McCullagh and Nelder 1989). Species that were positively associated with area were considered sensitive to fragmentation. All analyses were conducted using SAS statistical software (SAS Institute 1999).

NATURAL NESTS

In 1998 and 1999 nests of Swainson's Thrushes and Winter Wrens were monitored in plots established along forest/suburban edges and at locations distant (>400 m) from suburban edges (J. Kranz and T. L. George, unpubl. data). Nests were monitored at 3–4 day intervals until the nest failed or the young fledged. Daily Survival Rate (DSR) was computed for edge (<100 m from suburban edge) and interior (>100 m from suburban edge) nests using the Mayfield method (Hensler and Nichols 1981) and comparisons were performed using program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989). Because of small sample sizes of nests, we used $\alpha = 0.10$ to reduce the chance of a Type II error.

LITERATURE SURVEY

We surveyed the literature for studies of the response of diurnal landbirds to forest fragmentation in wet coniferous forests of the Pacific Northwest. We classified a species as area sensitive if its abundance increased with patch size (Schieck et al. 1995; this study) or with the amount of mature or old-growth forest within a surrounding buffer. Buffers differed in extent from 100 ha (Manuwal and Manuwal *this volume*) to 250–300 ha (McGarigal and McComb 1995). Rosenberg and Raphael (1986) examined both patch size and the amount of mature or old-growth in a 1,000-ha buffer surrounding the stand. Lehmkuhl et al. (1991) examined three scales: patch size, the area adjacent to the patch (within 400 m of the boundary), and the landscape (circular 2,025 ha area centered on the patch). Hejl and Paige (1994) compared bird relative abundance between a continuous stand of old-growth forest, an old-growth forest with 1–8 year-old clearcuts, and a selectively logged forest. A species was classified as edge sensitive if its abundance declined with proximity to edge (Brand and George 2001) or declined in abundance as the amount of edge increased in a surrounding buffer area. Buffer areas varied from 10 ha (Rosenberg and Raphael 1986), to 100 ha around each patch (Manuwal and Manuwal *this volume*), to 400 m surrounding the patch (Lehmkuhl et al. 1991). Thus there were seven studies that examined area effects and four that examined edge effects. We included fewer studies in our analysis than Manuwal and Manuwal (*this volume*, Table 1) because

we only included studies that specifically addressed area or edge sensitivity. Life history characteristics (nest type, migratory status, and foraging mode) of each species were obtained from the studies included in the summary and from the literature (Ehrlich et al. 1988). Species that showed evidence of area effects in two or more studies are included in Table 3.

RESULTS

Thirty-one species were included in the analysis of bird abundance and patch size (Table 1). Three species, the Golden-crowned Kinglet, Pacific-slope Flycatcher, and Wilson's Warbler, were detected in all of the patches. The abundances of six species, the Pileated Woodpecker, Pacific-slope Flycatcher, Brown Creeper, Steller's Jay, Winter Wren, and Varied Thrush, were positively correlated with log forest patch size (Table 2, Fig. 2). These species spanned the whole range of frequency values, from species that were detected in all of the patches (Pacific-slope Flycatcher) to those that were detected in a small proportion of the patches (Pileated Woodpecker). American Robins, Orange-crowned Warblers, Dark-eyed Juncos, and Song Sparrows were negatively correlated with patch size (Table 2, Fig. 2).

Varied Thrushes and Pileated Woodpeckers showed a threshold response to patch area. Varied Thrushes were detected in only 1 out of 17 patches below and 20 out of 21 patches above 16 ha. Pileated Woodpeckers were detected in 2 of 29 patches below and 6 of 9 patches above 48 ha. None of the other species showed evidence of a threshold response (Fig. 2).

Twenty-three Swainson's Thrush and 48 Winter Wren nests were monitored in the two years. Nest success for both years combined was low for Swainson's Thrushes (25%; DSR $\pm$ SE $= 0.940 \pm 0.016$), whereas Winter Wrens had high nest success (65%; 0.986 ± 0.016). Daily survival rate of Swainson's Thrush nests close (<100m) to forest edges was lower than interior nests (0.92 ± 0.023 vs. 0.974 ± 0.018, respectively; P $= 0.065$) but nest success of Winter Wrens did not differ between edge and interior locations (0.991 ± 0.0053 vs. 0.977 ± 0.009, respectively; P $= 0.17$). None of the nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*).

LITERATURE SURVEY

We found eight studies that had examined the effects of forest fragmentation on diurnal landbirds in Westside forests (Table 3). Because each study used different methods to examine these relationships and species composition varied among sites, the results must be interpreted cautiously. However, we felt this comparison was

TABLE 1.   BIRD SPECIES INCLUDED IN ANALYSES OF PATCH CHARACTERISTICS AND BIRD ABUNDANCE IN COASTAL REDWOOD FORESTS

Species	Proportion of patches occupied (N = 38)
Golden-crowned Kinglet (*Regulus satrapa*)	1.00
Pacific-slope Flycatcher (*Empidonax difficilis*)	1.00
Wilson's Warbler (*Wilsonia pusilla*)	1.00
Chestnut-backed Chickadee (*Poecile rufescens*)	0.97
Winter Wren (*Troglodytes troglodytes*)	0.95
Swainson's Thrush (*Catharus ustulatus*)	0.92
Brown Creeper (*Certhia americana*)	0.89
Steller's Jay (*Cyanocitta stelleri*)	0.89
American Robin (*Turdus migratorius*)	0.84
Hermit Warbler (*Dendroica occidentalis*)	0.82
Dark-eyed Junco (*Junco hyemalis*)	0.74
Song Sparrow (*Melospiza melodia*)	0.68
Orange-crowned Warbler (*Vermivora celata*)	0.66
Common Raven (*Corvus corax*)	0.63
Purple Finch (*Carpodacus purpureus*)	0.63
Pine Siskin (*Carduelis pinus*)	0.58
Vaux's Swift (*Chaetura vauxi*)	0.53
Varied Thrush (*Ixoreus naevius*)	0.47
Hutton's Vireo (*Vireo huttoni*)	0.42
Band-tailed Pigeon (*Columba fasciata*)	0.37
Northern Flicker (*Colaptes auratus*)	0.32
Red-breasted Nuthatch (*Sitta canadensis*)	0.32
Western Tanager (*Piranga ludoviciana*)	0.32
Cassin's Vireo (*Vireo cassinii*)	0.29
Hermit Thrush (*Catharus guttatus*)	0.26
Pileated Woodpecker (*Dryocopus pileatus*)	0.24

an important first step in identifying species that consistently show evidence of sensitivity to fragmentation.

Out of seven studies that examined area sensitivity, ten species were identified as being sensitive to fragmentation in two or more and seven in three or more studies (Table 3). There was no tendency for species with particular nest types or foraging modes to predominate, but the majority of the species were residents.

Eight of the ten species that were identified as area sensitive also showed evidence of edge sensitivity in one or more studies (Table 3). Thus, there is high concordance between area sensitive and edge sensitive species in these studies. The association between edge sensitivity and area sensitivity that we found, however, must be viewed with caution. Only one of the studies (Brand and George 2001) was specifically designed to examine response to forest edge; the others were based on point counts, which may be a poor indicator of edge effects (Villard 1998).

DISCUSSION

Six of the 31 bird species we examined in the forest patch size analysis showed a positive association with forest patch area, suggesting that a substantial portion of the avifauna is sensitive to the effects of forest fragmentation in this region. Four species, American Robins, Orange-crowned Warblers, Dark-eyed Juncos, and Song Sparrows, were more abundant in small than in large forest patches. This is consistent with the habitat associations of these species. Song Sparrows and Orange-crowned Warblers are more abundant in young second-growth than mature redwood forests (Hazard and George 1999) and therefore are likely to be associated with the edges of mature stands. American Robins and Dark-eyed Juncos are generally associated with forest openings (Ehrlich et al. 1988) and therefore it is not surprising that they are more abundant in smaller patches. Because of the extensive loss and fragmentation of mature and old-growth forest in this region, we will focus our discussion on those species that may be negatively affected by loss and fragmentation of mature and old-growth forests.

Other studies in Westside forests have failed to detect strong evidence for edge or area sensitivity among diurnal landbirds (Rosenberg and Raphael 1986, Lehmkuhl et al. 1991, McGarigal and McComb 1995, Schieck et al. 1995). The lack of evidence in other studies may have been due to the landscapes studied and the approaches

TABLE 2. POISSON REGRESSION RELATIONSHIPS BETWEEN BIRD RELATIVE ABUNDANCE AND PATCH AREA IN 38 REDWOOD FOREST PATCHES SURVEYED IN NORTHERN CALIFORNIA IN 1994

Species response to fragmentation	Slope ± SE	P
Negative		
Pileated Woodpecker	0.62 ± 0.25	0.015
Pacific-slope Flycatcher	0.08 ± 0.04	0.037
Steller's Jay	0.17 ± 0.07	0.029
Winter Wren	0.30 ± 0.05	<0.001
Brown Creeper	1.67 ± 0.09	0.055
Varied Thrush	0.71 ± 0.06	<0.001
Positive		
American Robin	−0.44 ± 0.11	<0.001
Orange-crowned Warbler	−0.76 ± 0.26	0.004
Dark-eyed Junco	−0.52 ± 0.24	0.029
Song Sparrow	−0.55 ± 0.27	0.043

Notes: Species that were positively related to area were classified as showing a negative response to fragmentation. Those showing the opposite trend were classified as being positively associated with fragmentation. Only those species that occurred in at least 20% of the patches were included in the analysis.

that were used. Lehmkuhl et al. (1991) and Rosenberg and Raphael (1986) studied landscapes that were far less fragmented than the redwood forests we examined. The smallest stand examined by Lehmkuhl et al. (1991) was 51 ha, and most of the area around the stands (2,025 ha) consisted of less than 50% clearcut. Few (4/46) of the stands that Rosenberg and Raphael (1986) studied were true islands (isolated from other mature stands by clearcuts or hardwood forest), and the amount of clearcut forest in the surrounding 1000 ha block varied from 0 to 44%. Thus the lack of evidence for sensitivity to fragmentation in these studies may be because the landscapes were not sufficiently fragmented to affect the bird species they examined. McGarigal and McComb (1995) specifically examined landscapes (250–300 ha) encompassing a wide range of landscape structure based on the proportion of late-seral forest and the spatial configuration of the forest. However, they did not use a patch-centered approach, but rather examined the relationship between landscape characteristics and average bird abundance in all seral stages within those landscapes. Thus, the scale of their analysis was much larger than our study. Schiek et al. (1995) used a similar approach to ours but their sample of patches was small (21), and therefore their ability to detect effects of fragmentation may have been limited.

We found no association between sensitivity to fragmentation and life history characteristics. However, most of the species were residents, which contrasts sharply with similar summaries of birds in the midwestern and eastern United States where species that have been identified as sensitive to fragmentation are more often long-distance migrants (Robbins et al. 1989b, Freemark et al. 1995). Thus, there does not appear

to be any suite of life history traits that makes a species more likely to be negatively affected by fragmentation in these forests. This suggests that attempts to classify sensitivity to fragmentation based on life history traits are likely to be problematical (Hansen and Urban 1992, Hansen et al. 1993).

Two species, Pileated Woodpeckers and Steller's Jays, showed evidence of area sensitivity but not edge sensitivity. Pileated Woodpeckers have large territories (>300 ha) in western coniferous forests (Bull and Holthausen 1993), and therefore small isolated forest patches may be less suitable for nesting and foraging. Hejl (1992) also found that Pileated Woodpeckers showed a threshold response to forest patch area in the northern Rockies and suggested that large stands or aggregates of small stands of late-seral forests are necessary to maintain suitable habitat for this species. Brand and George (2001) found that Steller's Jay abundance declined with distance from edge in redwood forests, which is inconsistent with their area sensitivity. Rosenberg and Raphael (1986) also found that Steller's Jays were more abundant along edges, and that they were weakly negatively associated with an index of insularity. Thus, the evidence for area sensitivity in Steller's Jays is weak in both studies (Rosenberg and Raphael 1986; this study), and therefore their designation as area sensitive may be a statistical artifact.

Eight of ten species that showed sensitivity to fragmentation also showed evidence of edge sensitivity. This suggests that area sensitivity may be related to edge avoidance in these species. Although edge sensitivity is often assumed to be associated with area sensitivity (Whitcomb et al. 1981, Askins et al. 1990, Freemark and Collins 1992), Villard (1998) found a poor cor-
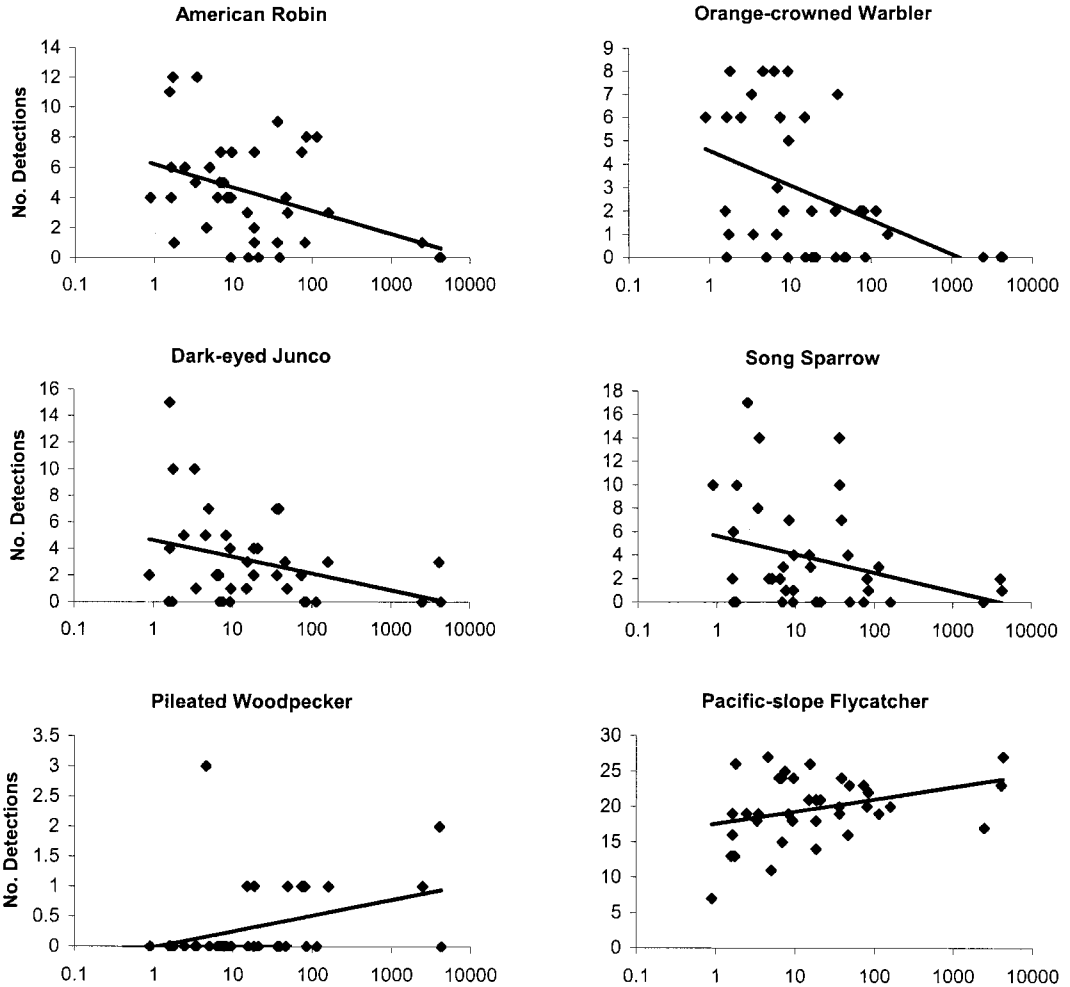
FIGURE 2.   Relationship between relative density and patch area for bird species in redwood (*Sequoia sempervirens*) forest patches in northern California. Species that show a positive correlation between patch area and relative abundance are considered area sensitive. Fitted line is best fit Poisson regression with log link function.

relation between edge- and area-sensitive species in studies conducted in the eastern United States.

There are many factors that change between forest edges and interior locations that may influence bird abundance, such as differences in predation (Paton 1994), microclimate (Chen et al. 1993), vegetation structure (Ranney et al. 1981), and insect composition (Shure and Phillips 1991). These factors may act singly or in combination to make forest edges more or less suitable to particular species. For instance, moisture gradients may influence the abundance of ground-dwelling arthropods, which in turn could affect the distribution of ground foraging bird species, as has been suggested for Ovenbirds (*Seiurus aurocapillus*; Gibbs and Faaborg 1990).

Reduced moisture along forest edges may play an important role in the edge avoidance for several of the species. 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 have broad habitat preferences in fall and winter, but that habitat selection shifts in the breeding season almost exclusively to old-growth forest characterized by a dense, moist understory. Likewise, McGarigal and McComb (1995) found that Winter Wrens are associated with riparian systems in Oregon. The Varied Thrush breeds in moist coniferous forest (George 2000) and song post locations are associated with large diameter trees, on steep slopes, surrounded by a high density of trees
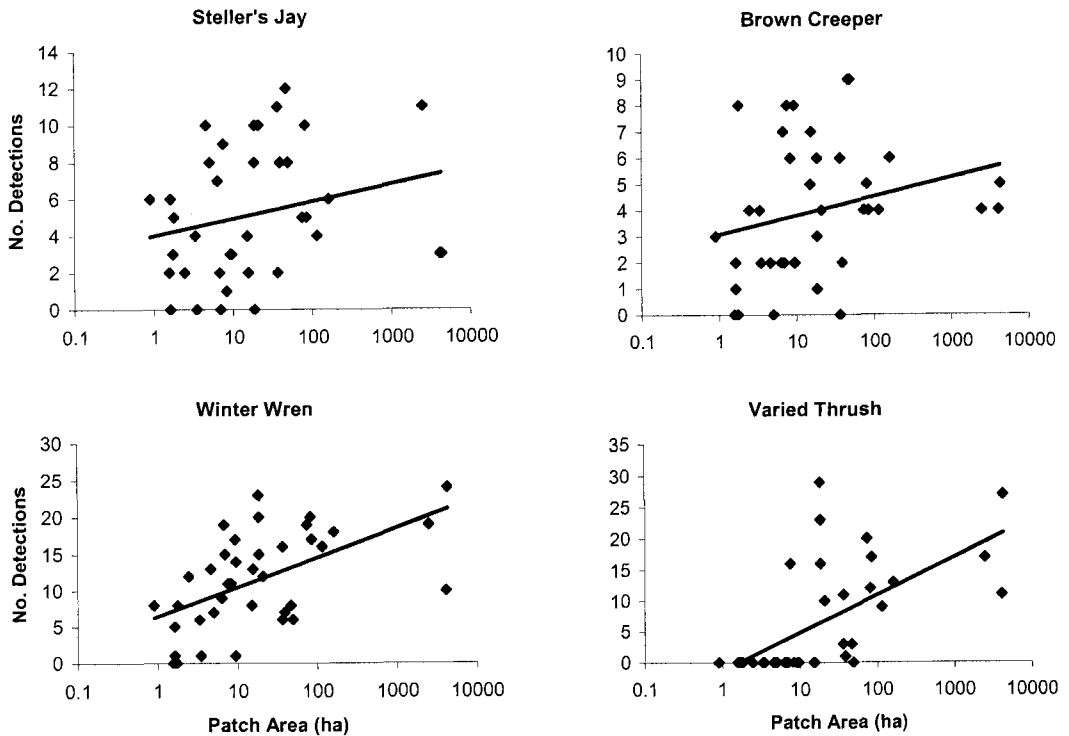
FIGURE 2.   Continued.

near streams (Beck and George 2000). Thus, male thrushes prefer moist, shady locations for song posts. The Pacific-slope Flycatcher breeds in forests, especially near water (Ehrlich et al. 1988). Edges receive higher levels of incident radiation (Chen et al. 1993), and thus the microclimate near edges may be unsuitable for these species. Microclimate changes, in turn, could af-

fect vegetation composition and structure as well as prey availability near edges.

Another factor that may cause bird species to avoid edges is predation (Brittingham and Temple 1983). The mechanism is less clear in this case but it could either be a direct response to the presence of potential predators along edges or occur indirectly as unsuccessful nesters move

TABLE 3.   BIRD SPECIES IDENTIFIED IN TWO OR MORE STUDIES AS SHOWING EVIDENCE OF SENSITIVITY TO FOREST FRAGMENTATION IN WET CONIFEROUS FORESTS OF THE PACIFIC NORTHWEST

Species	Nest type[a]	Migratory status[b]	Foraging mode[c]	Area sensitive[d]	Edge sensitive[d]
Pileated Woodpecker	Cavity	R	Drill	1, 3, 7	
Pacific-slope Flycatcher	Cup	L	Flycatch	6, 7	1, 8
Steller's Jay	Cup	R	Omnivore	1, 7	
Chestnut-backed Chickadee	Cavity	R	Foliage	1, 3, 5, 6	1, 6
Red-breasted Nuthatch	Cavity	R	Bark	3, 5, 6	1, 8
Brown Creeper	Crevice	R	Bark	3, 4, 7	1, 8
Winter Wren	Crevice	R	Ground	1, 2, 3, 4, 6, 7	1, 2, 8
Golden-crowned Kinglet	Cup	R	Foliage	4, 6, 7	1
Varied Thrush	Cup	S	Ground	3, 5, 6	8
Hermit/Townsend's Warbler	Cup	L/S	Foliage	1, 6	1

[a] Cavity-nest in tree cavities; Crevice-nest in niches and behind bark; Cup-open cup nesters.
[b] L-long-distance migrant; R-resident; S-short distance migrant.
[c] Bark-bark gleaner; Drill-excavates insects from dead wood; Flycatch-sallies for insects from a perch; Foliage-gleans insects from foliage; Ground-gleans insects from ground; Omnivore-feeds on a variety of food types.
[d] Studies included: 1–Rosenberg and Raphael (1986); 2–Lehmkuhl et al. (1991); 3–McGarigal and McComb (1995); 4–Hejl and Paige (1994); 5–Schieck et al. (1995); 6–Manuwal and Manuwal (*this volume,* Table 6); 7–this study; 8–Brand and George (2001).
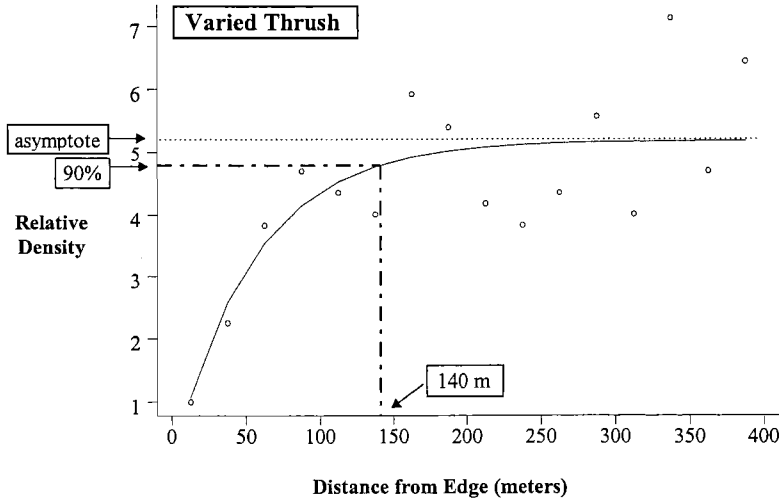
FIGURE 3.   Relative density with respect to distance from the forest edge and estimated edge width for the Varied Thrush. The points represent the band-specific relative density. The smooth curve represents the relative density based on an exponential regression model with one asymptote. The dash-dot line illustrates the edge width, defined as the distance from edge at which 90% of the asymptotic interior relative density has been achieved.

to new locations (Villard 1998). Brand and George (2000) found that predation on artificial nests that mimicked Varied Thrush and Winter Wren nests declined with distance from edge in redwood forest patches and that Steller's Jays were observed preying on the nests on several occasions. These results are consistent with the hypothesis that Winter Wrens and Varied Thrushes avoid forest edges because of higher nest predation. Steller's Jays are also more common on forest edges than forest interior locations (Brand and George 2001) and thus their presence could provide a proximate cue to nesting birds.

Other studies of artificial and natural nests have shown similar patterns with respect to distance from forest edge but there are many exceptions as well (Brand and George 2000, Sisk and Battin *this volume*). In addition, some studies suggest that predation rates on artificial nests may not reflect predation on real nests (Nour et al. 1993, Haskell 1995a, Willebrand and Marcstrom 1988, Wilson et al. 1998, Ortega et al. 1998, King et al. 1999). We found no difference in nesting success between edge (<100 m from forest edge) and interior (>100 m) nests for Winter Wrens, but nesting success of Swainson's Thrushes was lower on edges. Thus the pattern of decreasing nesting success with proximity to forest edge appears to be species-specific and more studies are needed to document the generality of this pattern.

Swainson's Thrush populations may be partic-

ularly vulnerable to increased predation along edges because thrushes are more abundant along edges in redwood forest patches (Brand and George 2001). Thus, thrushes may be experiencing an ecological trap (Gates and Gysel 1978) in this region, which could have severe effects on recruitment and population growth (Donovan and Lamberson 2001). Swainson's Thrush populations may be suffering poor recruitment in other parts of their range. Bednarz et al. (1998) found that Swainson's Thrushes are experiencing low nesting success in central Idaho, which they attributed to high levels of forest fragmentation in the region. Swainson's Thrushes have also been included in a draft list of species of special concern in California because of declines and a shrinkage of their breeding range in the Sierra Nevada mountains (T. Gardali, pers. comm.).

Regardless of the mechanism, edge avoidance has important implications for forest management. Information on the distance over which edge effects occur could provide important management guidelines for minimum widths of forest stands. Brand and George (2001) found that the distance to 90% of asymptotic interior relative density varied from 85 m for the Brown Creeper to 140 m for the Varied Thrush (Fig. 3). The average distance to 90% asymptotic density of the four forest interior species is approximately 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 2001). The edge widths estimated in Brand and George (2001) can be used to predict the patch sizes that may be suitable for particular forest interior species. For example, assuming that the average territory size for Varied Thrushes is 4 ha (George 2000), a circular patch of 19.6 ha would provide a 4 ha core with a 140 m buffer. Breeding Varied Thrushes were found to require a minimum patch size of approximately 16 hectares in coast redwood forests (Hurt 1996), close to the predicted size.

Another pattern that has been observed in studies in the eastern U.S. (Wilcove 1985) and Europe (Andrén et al. 1985, Angelstam 1986, Andrén and Angelstam 1988, Andrén 1992), is an increase in nest predation in forest fragments embedded within urban or agricultural landscapes as compared to regenerating forest or other more natural habitats. This may be due to an increase in generalist predators in landscapes that are dominated by agricultural or urban areas (Thompson et al. *this volume*). In redwood forest fragments, however, Brand and George (2000) found that rates of predation on artificial nests adjacent to rural (grassland) edge were significantly higher than nests located adjacent to suburbs, rivers, young forests, or roads. Thus, our results suggest that landscape context has a very different effect on rates of nest predation in the redwood region than in the eastern U.S. and Europe. Our results are consistent with those of Tewksbury et al. (1998) who found that rates of nest predation in riparian forests in Montana were higher in sites adjacent to undisturbed conifer forests than those adjacent to agricultural areas. Thus landscape context may not exert a predictable influence on rates of nest predation in western forests as it does in the eastern U.S. and Europe, perhaps due to the diversity of habitats and associated nest predators in the West. It is also possible that the various landscapes examined by Brand and George (2000) and Tewksbury et al. (1998) were not sufficiently different at the regional level to influence the predator community (Thompson et al. *this volume*).

Predation on artificial nests appears to be substantially lower in redwood forests than other forests. Approximately 69% of the artificial ground nests and 55% of the arboreal nests were intact after 14 days, which is substantially higher than has been found for most other studies conducted in fragmented forests of the eastern U.S. (Wilcove 1985, Yahner and Cypher 1987, Rudnicky and Hunter 1993, Whelan et al. 1994, Fenske-Crawford and Niemi 1997, Yahner and Mahan 1997). This difference may reflect lower overall avian abundance as well as lower predator activity in mature and old-growth redwood forests than in eastern deciduous forests.

Each of the species that showed evidence of area sensitivity in our survey also has been identified as an old-growth associate in one or more regions of the Pacific Northwest (Manuwal and Manuwal *this volume*, Table 2). This suggests that there may be an association between area sensitivity and dependence on old-growth forest habitat among the birds in this region. If this is the case, loss and fragmentation of old-growth forests may have a more severe impact on these species than predictions based on the area of old-growth forest alone.

EAST VS. WEST

The proportion of species showing evidence of sensitivity to habitat fragmentation in redwood forests (6/31 or 19%) is lower than the proportion that has been reported for studies in the eastern U.S. For example, Freemark and Collins (1992) reported that 34/70 or 49% of the species they examined showed evidence of area sensitivity, which is significantly higher than the proportion we observed ($\chi^2 = 7.67$, df = 1, P = 0.006). The proportions may change depending on what bird orders are included and the studies considered, but the pattern of a higher proportion of area sensitive species in forests of the eastern and midwestern U.S. relative to redwood forests is unlikely to change. In addition, given the overlap in species identified as area sensitive in the studies we examined, it is likely that this pattern holds for all Westside forests. We also found few long-distance migrants among the species that are area sensitive, which is very different from the eastern and midwestern U.S. where long-distance migrants predominate.

Our studies also suggest that the ecological processes that are responsible for area sensitivity among redwood forest birds may differ from those in the eastern U.S. Thompson et al. (*this volume*) have proposed a "top-down" hierarchical model where higher agricultural and human habitation at the regional scale results in increased predator and parasite numbers which in turn reduces the nesting success of birds in these landscapes. Contrary to the predictions of this model, we found that predation on artificial nests was significantly higher along natural grassland edges than suburban edges or roads. In addition, although predation on artificial nests declined with distance from forest edge, this pattern differed among species when we examined natural nests. Parasitism also was not a factor as none of the nests we monitored were parasitized by Brown-headed Cowbirds. Our studies suggest that area sensitivity in some species may be a result of edge avoidance and subsequent decline
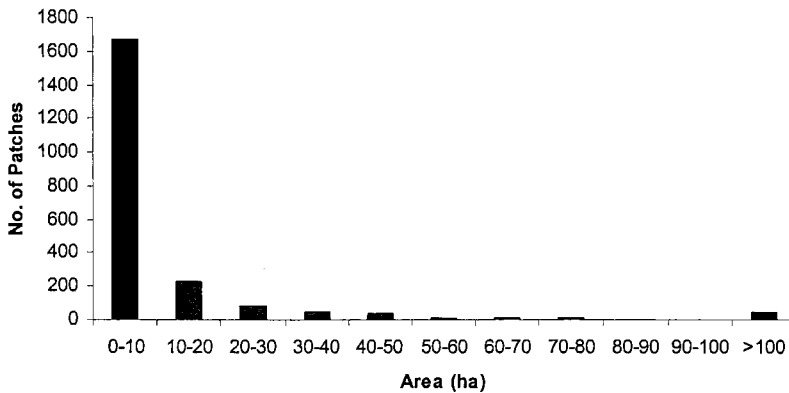
FIGURE 4.   Size distribution of mature and old-growth redwood (*Sequoia sempervirens*) forest patches north of Point Reyes National Seashore. Based on Landsat satellite images (Fox 1997).

in small forest patches. This suggests a "bottom-up" mechanism where behavioral responses to edge result in changes in abundance in different sized patches.

MANAGEMENT IMPLICATIONS

Several bird species that breed in coast redwood forests are negatively affected by forest fragmentation. This means that the regional abundance of these species will be affected not only by the amount of mature and old-growth forest but also its distribution across the landscape. Most redwood forests are privately owned and are intensively managed for timber production, and it is unlikely that large amounts of land will be added to parks and reserves (Thornburgh et al. 2000). Thus, the abundance of these species in the region will be greatly influenced by how forest practices affect the distribution of mature forests across the landscape. Presently, 79% of the mature and old-growth redwood forest patches north of Point Reyes National Seashore are less than 10 ha (Fig. 4). This

is below the threshold for breeding occupancy by Varied Thrushes, and many of these patches may be poor or unsuitable habitat for the other species that are sensitive to fragmentation. Changes in forest practice rules that result in larger patches of mature forest on the landscape would greatly benefit these species and should be encouraged.