

BREEDING BIRD RESPONSE TO RIPARIAN BUFFER WIDTH IN MANAGED PACIFIC NORTHWEST DOUGLAS-FIR FORESTS

SCOTT F. PEARSON^{1,2} AND DAVID A. MANUWAL¹

¹College of Forest Resources, P.O. Box 352100, University of Washington, Seattle, Washington 98195 USA

Abstract. We examined the relative importance of riparian vs. upland habitats to breeding birds by comparing species abundance, richness, and similarity of bird communities in managed Douglas-fir forests in western Washington State, USA. We also examined whether forested buffer strips along second- and third-order streams effectively maintain the pre-logging riparian breeding bird community by comparing species abundance, richness, and turnover among three treatments: (1) unharvested controls; (2) sites that were clear-cut, leaving a narrow (~14 m) forested buffer on both sides of the stream; and (3) sites that were clear-cut, leaving a wide (~31 m) forested buffer along both sides of the stream.

Deciduous trees, berry-producing shrubs, and other deciduous shrubs less common in adjacent upland forest characterized streamside zones. Despite different vegetation features, riparian and upland habitats did not differ in any measures of bird species richness and composition. No species or species group was more abundant in the upland. Neotropical migrants, resident species, and species associated with deciduous trees and shrubs in forested habitats were more abundant in riparian habitats than in adjacent uplands. Total bird abundance and abundance of four species (American Robin [*Turdus migratorius*], Pacific-slope Flycatcher [*Empidonax difficilis*], Black-throated Gray Warbler [*Dendroica nigrescens*], and Winter Wren [*Troglodytes troglodytes*]) were higher in riparian habitats. Abundance of these riparian associates was correlated with percent cover of berry-producing shrubs and the number of deciduous trees in the canopy.

We found that the number of breeding bird species on sites with narrow buffers increased from slightly fewer than controls before harvest to an average of 10 more species than controls after harvest, a change reflected in an average 20% increase in species turnover on narrow-buffer sites relative to controls. Total bird abundance did not differ between treatments and controls. Resident species, those species associated with shrubs in forested habitats and conifer trees, declined on both buffer treatments. Species associated with upland and riparian forests (Black-throated Gray Warbler, Golden-crowned Kinglet [*Regulus satrapa*], and Brown Creeper [*Certhia americana*]) decreased in abundance on riparian buffer treatments relative to controls, whereas species associated with open, shrubby habitats (Dark-eyed Junco [*Junco hyemalis*], Cedar Waxwing [*Bombycilla cedrorum*], and Song Sparrow [*Melospiza melodia*]) increased in abundance on one or both riparian buffer treatments.

High species turnover on narrow-buffer treatments indicated that buffers <14 m on each side of the stream did not maintain the pre-logging bird community. There was little difference in species turnover or species richness between the wide-buffer treatment and the control, indicating that a 30-m buffer on both sides of second-order and third-order streams maintains most of the pre-logging bird community in the first two years postharvest. The Black-throated Gray Warbler was the only riparian associate to decline on both the narrow- and wide-buffer treatments; its abundance was positively correlated with buffer width, and a buffer ≥ 45 m wide on each side of second- and third-order streams was needed to support populations at densities found on unharvested controls. To maintain the entire breeding bird community associated with forested riparian habitats in the coastal Northwest, we recommend a minimum buffer of 45 m along both sides of second- and third-order streams. Habitat features such as deciduous trees (*Alnus rubra* and *Acer macrophyllum*) and berry-producing shrubs (especially *Rubus spectabilis*) appear to be important and should be maintained within forested riparian buffer strips.

This study documents short-term effects of riparian treatments on the breeding bird community, which may take several years to respond to habitat manipulations. Thus, we recommend continued monitoring to assess long-term effects of buffer width reduction.

Key words: American Robin; bird species richness; Black-throated Gray Warbler; breeding bird density; Douglas-fir forest; Pacific-slope Flycatcher; riparian bird community; riparian buffer width; riparian forest management; species turnover; Winter Wren.

INTRODUCTION

Riparian zones are ecotones between terrestrial and aquatic environments, and represent some of the most

dynamic portions of the landscape (Swanson et al. 1988). As a consequence, riparian zones typically are more structurally diverse and more productive than adjacent uplands (Bull 1978), and usually support a greater number of plant (Gregory et al. 1991) and vertebrate (Thomas et al. 1979, Oakley et al. 1985) species. In arid regions of the western United States, riparian habitats make up <1% of the landscape, yet 82% of all bird species breeding in northern Colorado occur in riparian vegetation (Knopf 1985), and 51% of all bird

Manuscript received 10 September 1999; revised 20 March 2000; accepted 19 April 2000; final version received 8 May 2000.

² Present address: Washington Department of Natural Resources, Lands and Resources Division, Box 47016, 1111 Washington St. S.E., Olympia, Washington 98504-7016 USA. E-mail: scott.pearson@wadnr.gov

species in southwestern states are completely dependent upon this habitat type (Johnson et al. 1977). This high species richness may result from higher food resources, such as insects and other invertebrates (Jackson and Fisher 1986, Gray 1993), and more diverse and complex vegetation (Bull and Skovlin 1982) that provides many potential nest sites.

In regions where the contrast between riparian and upland habitats is less pronounced, there may be little or no difference in bird species richness and abundance between the two habitats (Murray and Stauffer 1995). In the relatively wet and lush forests of the Pacific Northwest, bird species richness and abundance may even be higher in upland than in riparian habitats (McGarigal and McComb 1992). Thus, the relative importance of riparian zones to terrestrial wildlife appears to vary geographically.

Throughout most of North America, buffer strips of standing trees are left between clearcuts and aquatic habitats (Knopf et al. 1988). Buffer strips are left to protect water quality and to minimize adverse effects of harvest on aquatic species and the terrestrial species associated with riparian habitats. In addition, buffer strips may serve as important connections between fragmented habitats and, consequently, may counteract some of the problems associated with landscape fragmentation (Wilcox and Murphy 1985, Saunders et al. 1991, Schmiegelow et al. 1997). A critical question associated with riparian zone management is how wide should riparian buffers be to protect the species that depend on these habitats? Several studies have demonstrated a positive correlation between species richness and abundance and width of the buffer (Stauffer and Best 1980, Darveau et al. 1995, Spackman and Huges 1995, Kilgo et al. 1998, Hagar 1999). Buffer width also appears to affect microclimatic conditions within the riparian zone (Brosfokske et al. 1997) that may, in turn, influence the plant and animal community found there. Consequently, manipulating the width of forested riparian buffers left after clear-cutting the adjacent uplands has important implications for preserving biological diversity (Spackman and Huges 1995).

Investigators have used a variety of approaches to evaluate the effect of buffer width on bird species richness and abundance. Some have looked at the change in species richness as one moves away from the stream in unharvested forests (e.g., Spackman and Huges 1995, Wiebe and Martin 1998). Others have correlated buffer width with bird abundance and richness after timber harvest (Kinley and Newhouse 1997, Hagar 1999, Whitaker and Montevecchi 1999). Few studies have used an experimental approach to examine the effect of buffer width on wildlife (but see Darveau et al. 1995). For many studies, it is difficult to evaluate the effect of buffer width on species that depend upon riparian zones, because few have first attempted to identify the species associated with riparian habitats (but see Wiebe and Martin 1998, Whitaker and Montevecchi 1999). As a consequence, the species

that decline or disappear in narrow riparian buffers may not be species that depend upon riparian zones for reproduction or survival.

This study has two objectives: (1) to determine which species, if any, are associated with riparian habitats in the coastal and Cascade mountains of western Washington State; and (2) to assess the effect of forested buffer width on the breeding bird community after the uplands have been clear-cut. To accomplish these objectives, we compared species abundance, richness, and similarity between riparian and adjacent upland habitats before timber harvest. After timber harvest, we compared species abundance, richness, and turnover in the riparian zones of unharvested sites (controls) with two treatments: sites where the uplands were clear-cut, leaving a narrow (~14 m) forested riparian buffer on both sides of the stream; and sites where the uplands were clear-cut, leaving a wide (~31 m) forested buffer along each side of the stream.

METHODS

Study area and experimental design

The experiment was conducted on the west side of the southern Cascade Mountains and the coast range of Washington between the Cedar River watershed (east of Seattle) to the north and the Columbia River to the south. All sites were located in the Western Hemlock forest zone (Franklin and Dyrness 1973). Forests in this zone are dominated by conifers including Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Deciduous tree species are not common in this zone except in recently disturbed sites and riparian habitats. Riparian habitats in this region are dominated by red alder (*Alnus rubra*) and big-leaf maple (*Acer macrophyllum*) in early seral stages and by western hemlock and redcedar in later stages. Ridges and steep valleys characterize the region, and the climate consists of warm, dry summers and cool, wet winters. The lands used in this research are owned by the state of Washington, the city of Seattle, and private timber companies (see *Acknowledgments*). The primary management objective on these lands is the production of even-aged conifer plantations dominated by Douglas-fir.

Eighteen sites were selected according to the following criteria: (1) low elevation <620 m; (2) second-growth forest 45–65 yr old; (3) dominated by Douglas-fir and western hemlock in the uplands; (4) containing a second- or third-order stream (Strahler 1957); (5) predominantly coniferous riparian canopy with deciduous tree component; and (6) at least 500 m in stream length. Site size ranged from ~33 ha to 50 ha, and each site was located along a different stream. Each of the 18 selected sites was assigned to one of three treatments, resulting in six replicate sites of control, narrow-buffer treatment, and wide-buffer treatment. Both treatments consisted of forested riparian buffers along both

sides of the stream and clear-cut uplands. The narrow-buffer sites were harvested according to Washington State Forest Practice Board (1992) regulations, which specify a minimum riparian buffer of 8 m along each side of the stream. After harvest, the mean buffer width on the narrow-buffer treatments ranged from 7.3 to 23.2 m. Wide-buffer treatment consisted of a wider and more variable forested buffer along each side of the stream. These wide buffers were intended to accommodate local features such as seeps and structural components such as snags and downed wood, resulting in not only a wider buffer, but also a more variable buffer width (ranging from 20.6 to 47.9 m). After harvest, the clear-cut on each side of the stream ranged in size from 14 to 16 ha on both treatments. Preharvest data were collected in the spring of 1993 and postharvest data were collected in the springs of 1995 and 1996; no sampling occurred in 1994 when sites were logged. One narrow-buffer treatment site was not logged, resulting in six control sites, six wide-buffer sites, and five narrow-buffer sites for all analyses of treatment effects. We used all 18 sites for the riparian and upland habitat and bird community comparisons before harvest.

Bird sampling

Birds were surveyed using 15-m fixed-radius point counts (Verner 1985). In each site, five riparian stations were established along each side of the stream and five upland stations were established on each side of the stream, resulting in 10 riparian and 10 upland point-count stations per site. Each riparian station was located 15 m from the usual high water line, 100 m from other stations, and ≥ 50 m from the edge of the site. Each upland station was located parallel to and 100 m upslope from the riparian stations. Reference flags were placed 15 m from each side of each station. Censuses started within 30 min of dawn and were completed within 5 h. Upon arriving at a survey point, observers remained stationary and quiet for a minimum of 1 min to allow birds to settle, and then recorded all birds heard or seen during a 6-min period. To avoid biases among observers, observers were rotated among the 18 study sites. To avoid biases associated with always visiting riparian or upland sites first, we alternated travel routes. Each site was visited six times between mid-April and late-June. The surveys were evenly spaced throughout the breeding season to account for differences in breeding phenology among species. No survey was conducted during heavy precipitation or high winds. Every attempt was made to avoid counting individual birds more than once. If the riparian buffer was narrower than the diameter of our point-count circle on harvested sites, then we recorded whether the bird was detected in the forested buffer or in the clear-cut portion of the circle.

Small-radius point counts were used because it was difficult to travel along streams with steep slopes (some $>40^\circ$) and dense vegetation. Small-radius point counts eliminated the problem caused by steam noise: differ-

ences in the ability to detect birds along riparian and upland habitats. Small-radius point counts also allowed us to examine differences in bird abundance along narrow strips of forested habitat after harvest.

Habitat sampling

Vegetation sampling occurred once prior to timber harvest and once following timber harvest on all 18 sites. To measure habitat variables at each site, we established a total of 12 vegetation plots (16×20 m) along the riparian zone and 10 vegetation plots in the uplands. The riparian vegetation plots were systematically centered on six of the 10 riparian point-count stations and six points halfway between riparian stations. The upland vegetation plots were systematically centered on six of the 10 upland point-count stations and four points halfway between point-count stations. More riparian plots were established to account for the more complex riparian vegetation relative to the even-aged, conifer-dominated uplands. Each vegetation plot was oriented such that the 20-m side of the plot was parallel to the stream. All trees >3 m tall and clusters of vine maple trees (*Acer circinatum*) were counted within the entire plot. Counts of trees other than vine maple were grouped as Douglas-fir/true fir (*Abies*), western hemlock/western redcedar, or deciduous trees. These groupings were based on natural species associations and habitat conditions. Western hemlock and redcedar are associated with cool and wet conditions, whereas Douglas-fir and true fir are associated with drier conditions. Deciduous trees are associated with riparian habitats and recently disturbed areas. All snags >1.5 m tall and 10 cm diameter (measured 1.4 m above the ground) were counted within the entire plot. Within each vegetation plot, we delineated four 8×10 m quadrants. Percent cover of shrubs 1–3 m tall and logs >10 cm diameter were estimated in two quadrants within each plot (the right half of the plot as you face upslope from the stream). Canopy cover was measured at the center and the four corners of the plot using a spherical densiometer (Lemmon 1957). At each of the five sampling points, we took one densiometer reading facing the stream, one facing away from the stream, one facing upstream, and one facing downstream. Buffer width was measured at each riparian point-count station by measuring the perpendicular ground distance between the stream edge and the outermost tree.

Data analyses

Bird abundance.—We excluded from all analyses individuals that flew over the site, migrants that did not breed in the area (e.g., Ruby-crowned Kinglet [*Regulus calendula*] and Golden-crowned Sparrow [*Zonotrichia leucophrys*]), and all species not adequately sampled by point counts (grouse, raptors, corvids, and waterfowl). Finally, to avoid including nonbreeders in our analyses, we excluded all species that were not detected on at least two occasions.

To compare individual species abundance, we used an index of abundance for each common species. Common species were detected >15 times and detected on at least half of the sites in the preharvest year, or were detected >15 times and on at least four of the sites in one of the two postharvest years. A separate index of abundance was developed for riparian and upland habitats and was calculated by dividing the total number of detections per site and year by the number of censuses in a given year ($n = 6$).

We used paired t tests to compare overall abundance, abundance of individual species, and abundance of species groups between the riparian and upland habitats in each of the 18 sites in the preharvest year (1993). We examined the relationship between abundance of riparian associated species and habitat variables in the pre-harvest year using an interactive stepwise linear regression. We examined the effect of buffer width on species abundance using a multivariate repeated-measures ANOVA. A significant treatment \times year interaction indicated that birds responded differently to the treatments over time. When the treatment \times year interaction was significant (Wilks' lambda), univariate ANOVA and Tukey pairwise comparisons were used to examine differences among treatments. Because there was strong annual variation in abundance and low statistical power for the species not demonstrating a treatment \times year interaction (see *Results*), we also used a univariate F test to examine treatment effects for these species. For the two species not detected in the preharvest year (Table 1), we used only the two postharvest years in the repeated-measures ANOVA and looked for treatment rather than treatment \times year effects. Equation 13.13 (Zar 1984) was used to estimate the power of the repeated-measures ANOVA in detecting an interaction effect. We used a linear regression to compare the mean abundance of riparian-associated species for the two years postharvest with buffer width on logged sites after harvest. When abundance of any given species declined on harvested sites and there was a positive relationship between buffer width and bird abundance, we used the mean number of detections on controls for the two postharvest years to derive an estimate of the buffer width necessary to maintain abundance levels similar to that of unharvested controls. We accomplished this by marking the mean ± 1 SE values for the unharvested controls (in the postharvest years) on the abundance axis (y -axis) in Fig. 2 and extending a horizontal line from these values to the regression line. From each of the intersections between these horizontal lines and the regression line, we dropped a vertical line down to the buffer width (x -) axis to determine our recommended minimum, maximum, and mean buffer width values.

We compared abundance between riparian and upland habitats before harvest and the riparian treatment effect postharvest for the following species groupings: (1) species associated with the canopy of coniferous

forests; (2) species associated with deciduous trees; (3) species associated with shrubs and small trees in open habitats; (4) species associated with shrubs and small trees in forested habitats; (5) cavity nesters; and (6) species grouped according to migratory status (neotropical migrants, short-distance migrants, and residents). For species group membership, see Table 1. Not all species were put into a habitat group (1–5), and habitat groupings were based on the primary use of these habitats for breeding and/or foraging (Carey et al. 1991, Gilbert and Allwine 1991, Manuwal 1991, McGarigal and McComb 1995, Manuwal and Pearson 1997). Cavity nesters included species that only used cavities for nesting. Winter Wren was not included in cavity nesters because we found it frequently nesting in root wads and other substrates. We examined the potential influence of our treatments on species grouped by habitat use because riparian habitats usually have higher diversity and density of deciduous shrubs (McGarigal and McComb 1992, Wiebe and Martin 1998) and trees (McGarigal and McComb 1992). We examined the potential influence of our treatments on species grouped by migratory pattern because residents and neotropical migrants may be sensitive to fragmentation, and because a number of neotropical migrants may prefer deciduous habitats (Welsh and Loughheed 1996). We compared treatment effects and associations with riparian and upland habitats for these species groups, using the same methods as described for individual species.

Bird species richness and turnover.—It is often difficult to count all species within any given area. Consequently, counts of species detected often underestimate the numbers of species present and create problems when comparing species richness between communities (Nichols et al. 1998a). In this study, it is unlikely that we detected all species because it was necessary to use small-radius point counts. To account for detection problems, we followed the methods of Nichols et al. (1998a, b) to estimate species richness and turnover for all comparisons. These methods use data on the presence or absence of each species at different sampling locations to estimate the number of species not detected at any location. All computations were conducted with program COMDYN, which uses the methods of Nichols et al. (1998a, b) and which was developed by Hines et al. (1999). This program produces a series of community-based estimates that can be used to compare communities at different times or in different areas. The equations used by COMDYN do not require catching and marking individual animals and are appropriate for point-count data (Nichols et al. 1998b). Estimates produced by COMDYN include species richness by location, relative richness, species co-occurrence, the number of species at one location or time that do not occur at another location or time, and the probability of species detection (Nichols et al. 1998b). The model used by COMDYN assumes that

TABLE 1. Detection rate (mean, with 1 SE in parentheses) of common species and species grouped according to migratory pattern and habitat associations in riparian habitats by treatment and year.

Species	Migration†	Habitat‡	Preharvest 1993			Postharvest 1995
			Control <i>n</i> = 6	Wide <i>n</i> = 6	Narrow <i>n</i> = 5	Control <i>n</i> = 6
Individual species						
Chestnut-backed Chickadee	R	C, CAV	3.13 (0.53)	2.57 (0.28)	4.16 (0.76)	0.70 (0.18)
Winter Wren	R	SC	3.07 (0.53)	3.33 (0.47)	2.58 (0.25)	3.7 (0.36)
Pacific-slope Flycatcher	NTM	D	2.13 (0.24)	2.03 (0.20)	1.58 (0.27)	3.23 (0.17)
Golden-crowned Kinglet	R	C	1.07 (0.35)	0.67 (0.25)	1.29 (0.32)	0.77 (0.37)
Wilson's Warbler	NTM	SC	0.67 (0.32)	0.67 (0.34)	0.44 (0.33)	1.10 (0.35)
Swainson's Thrush	NTM		0.20 (0.09)	0.20 (0.10)	0.28 (0.20)	0.53 (0.12)
Brown Creeper	R	C	0.13 (0.07)	0.13 (0.04)	0.12 (0.08)	0.23 (0.10)
Black-throated Gray Warbler	NTM	D	0.20 (0.10)	0.33 (0.15)	0.18 (0.05)	0.27 (0.07)
American Robin	SDM	D	0.30 (0.13)	0.23 (0.17)	0.0	0.13 (0.09)
Rufous Hummingbird	NTM		0.0 (0.0)	0.17 (0.13)	0.04 (0.04)	0.07 (0.07)
Cedar Waxwing	SDM	SO	0.0	0.0	0.0	0.0
Dark-eyed Junco	SDM		0.0	0.0	0.0	0.0
Hairy Woodpecker	R	CAV	0.0 (0.0)	0.03 (0.03)	0.05 (0.05)	0.23 (0.10)
Western Tanager	NTM		0.03 (0.03)	0.13 (0.08)	0.0	0.03 (0.03)
Warbling Vireo	NTM	SO	0.07 (0.07)	0.0	0.0	0.17 (0.17)
Song Sparrow	SDM	SO	0.0	0.03 (0.03)	0.0	0.0
Mean abundance/site			11.03 (0.85)	10.53 (1.19)	10.72 (1.03)	11.27 (0.62)
Species groups						
Neotropical migrants			3.33 (0.59)	3.53 (0.68)	2.52 (0.56)	5.4 (0.57)
Short-distance migrants			0.30 (0.13)	0.27 (0.20)	0.0	0.13 (0.10)
Residents			7.40 (0.58)	6.73 (0.43)	8.20 (0.60)	5.73 (0.30)
Species associated with habitats						
Conifer trees			4.33 (0.75)	3.37 (0.48)	5.57 (0.79)	1.70 (0.40)
Deciduous trees			2.63 (0.37)	2.60 (0.41)	1.76 (0.28)	3.63 (0.26)
Shrubs in open habitats			0.07 (0.07)	0.03 (0.03)	0.0	0.17 (0.17)
Shrubs in forested habitats			3.73 (0.52)	4.0 (0.78)	3.02 (0.24)	4.80 (0.60)
Cavities			3.13 (0.53)	2.60 (0.28)	4.21 (0.79)	1.03 (0.25)

Notes: Treatments include sites that were not harvested (control), harvested with a wider riparian buffer (wide), or harvested with a narrower riparian buffer (narrow). We report *F* and *P* values from a multivariate repeated-measures ANOVA examining year × treatment interaction (*Y* × *T*) and from univariate *F* tests examining treatment effects by year. Statistical tests were only performed for common species (see *Methods*).

† Migratory pattern: NTM, neotropical migrant; SDM, short-distance migrant; R, resident.

‡ Habitat association: C, conifer trees; D, deciduous trees; SO, shrubs and small trees in open habitats; SC, shrubs and small trees in forest habitats; CAV, cavity nester.

detection probability is heterogeneous among species (Nichols et al. 1998b). With the exception of three riparian habitats on control sites, the heterogeneity model adequately fit all other sites (*n* = 21, all *P*'s > 0.05). Despite a lack of fit in three cases, the estimators derived should perform much better than ad hoc estimators (Nichols et al. 1998b). We used Eq. 3 in Nichols et al. (1998a) to estimate the rate of change in species richness (the relative species richness in the riparian and upland comparison) between years because there were no differences in detection probabilities (all *P*'s > 0.05) between years or habitats. For all estimators, we report the jackknife estimator that is derived using a bootstrap approach. Bootstrap variance estimates were calculated using 200 iterations and a random seed. Initial fit of the data to the heterogeneity model was calculated using a goodness-of-fit (GOF) test. For this analysis, we excluded all species that were detected fewer than three times, that did not breed in the area, and that were not adequately sampled by point counts.

Habitat analyses.—For all habitat analyses, we used

total counts of trees and snags, mean percent cover of shrubs, logs, and canopy cover, and mean buffer width in the riparian and/or upland habitat for each site. We used discriminant analysis to discriminate between habitat features associated with the riparian habitats and those associated with the adjacent upland on all 18 sites before timber harvest. We used a paired *t* test to compare individual habitat variables between riparian and upland transects on all 18 sites before harvest. We used a two-sample *t* test to compare upland habitat variables between the two treatments postharvest. We used a multivariate ANOVA to compare habitat variables between treatments and controls postharvest. We used a two-sample *t* test to compare buffer width between the two treatments postharvest.

For all analyses, data not meeting the assumptions of normality (Kolmogorov-Smirnov one-sample test) or homogeneity of group variances (Bartlett's *F* test, residual scatter plots) were log- or arcsine-transformed (Zar 1984). When analyzing vegetation data, we used an alpha level of 0.05 because of large samples sizes

TABLE 1. Extended.

Postharvest 1995			Postharvest 1996				
Wide <i>n</i> = 6	Narrow <i>n</i> = 5	Univariate <i>F</i> (<i>P</i>)	Control <i>n</i> = 6	Wide <i>n</i> = 6	Narrow <i>n</i> = 5	Univariate <i>F</i> (<i>P</i>)	Y × T <i>F</i> (<i>P</i>)
0.40 (0.15)	0.88 (0.45)		0.64 (0.16)	0.86 (0.17)	0.40 (0.25)		2.7 (0.05)
3.97 (0.53)	3.52 (0.45)		1.75 (0.29)	1.28 (0.20)	1.00 (0.26)		
2.87 (0.30)	2.76 (0.33)		1.56 (0.39)	0.97 (0.17)	0.83 (0.15)		
0.10 (0.07)	0.04 (0.04)	3.13 (0.08)	0.39 (0.11)	0.0	0.07 (0.07)	7.79 (0.01)	
1.37 (0.17)	0.28 (0.19)	4.62 (0.03)	0.33 (0.18)	0.72 (0.19)	0.27 (0.17)		
0.83 (0.30)	0.44 (0.19)		0.17 (0.14)	0.28 (0.15)	0.07 (0.07)		
0.17 (0.08)	0.04 (0.04)		0.25 (0.13)	0.0	0.0	3.49 (0.06)	
0.07 (0.07)	0.0	5.72 (0.02)	0.06 (0.04)	0.03 (0.03)	0.0		3.40 (0.02)
0.60 (0.23)	0.40 (0.06)		0.31 (0.13)	0.47 (0.16)	0.67 (0.19)		3.6 (0.02)
0.18 (0.06)	0.16 (0.04)		0.11 (0.14)	0.25 (0.09)	0.30 (0.22)		
0.10 (0.07)	0.44 (0.26)	2.73 (0.10)	0.0	0.31 (0.11)	0.13 (0.13)	2.76 (0.10)	5.91 (0.01)
0.47 (0.10)	0.76 (0.37)	3.85 (0.05)	0.19 (0.11)	0.31 (0.08)	0.77 (0.34)		
0.30 (0.05)	0.52 (0.17)		0.25 (0.13)	0.28 (0.11)	0.07 (0.07)		
0.33 (0.11)	0.08 (0.05)	4.74 (0.03)	0.03 (0.03)	0.19 (0.11)	0.03 (0.03)		
0.83 (0.29)	0.76 (0.37)		0.08 (0.08)	0.42 (0.18)	0.10 (0.07)		2.4 (0.07)
0.27 (0.20)	0.56 (0.34)		0.0	0.44 (0.19)	1.17 (0.49)	4.38 (0.03)	2.15 (0.10)
12.93 (0.62)	11.64 (1.92)		6.14 (0.57)	6.81 (0.71)	6.03 (0.94)		
6.47 (0.45)	4.48 (1.01)		2.33 (0.60)	2.86 (0.41)	1.60 (0.55)		
1.47 (0.33)	2.16 (0.82)	4.88 (0.03)	0.53 (0.20)	1.53 (0.37)	0.14 (0.06)	16.63 (0.00)	7.88 (0.00)
5.00 (0.61)	5.00 (0.93)		3.28 (0.43)	2.42 (0.30)	1.53 (0.37)	5.33 (0.02)	2.8 (0.05)
0.67 (0.23)	0.96 (0.48)		1.28 (0.19)	0.86 (0.17)	0.47 (0.23)	4.25 (0.04)	2.48 (0.06)
3.53 (0.53)	3.16 (0.32)		1.92 (0.47)	1.47 (0.30)	1.50 (0.19)		
1.23 (0.42)	1.76 (0.93)		0.11 (0.08)	1.17 (0.36)	1.57 (0.54)	4.56 (0.03)	2.05 (0.10)
5.33 (0.42)	3.80 (0.74)		2.08 (0.20)	2.00 (0.20)	1.27 (0.33)	3.24 (0.07)	
0.77 (0.14)	1.40 (0.52)		0.89 (0.24)	1.14 (0.26)	0.47 (0.25)		2.36 (0.08)

and associated high power. When analyzing bird abundance, we used an alpha level of 0.10 because of small sample sizes and associated low power.

RESULTS

Riparian and upland habitat before harvest

We used the habitat variables in Table 2 to discriminate between upland and riparian habitats in the preharvest year. Discriminant analysis successfully separated riparian habitats, predicting group membership correctly in 94% of the cases; one of the 18 riparian transects was misclassified as an upland transect and one of the 18 upland transects was misclassified as a riparian transect. Riparian habitats had more deciduous trees <50 cm in diameter, whereas upland habitats had more Douglas-fir trees >50 cm in diameter, higher percent cover of evergreen shrubs, and higher canopy closure (Table 3). Paired *t* tests between riparian and upland habitats indicated that riparian habitats had more deciduous trees and shrubs and more berry-producing shrubs than did upland habitats (Table 2). Upland habitats had higher canopy closure, more snags, and more Douglas-fir/true fir trees than did riparian habitats (Table 2). Habitat variables measured along the riparian transects in the preharvest year were similar among treatments ($F = 0.96$; $df = 26, 4$; $P = 0.596$).

Riparian and upland bird community before harvest

Community comparisons.—There was no difference in bird species richness between riparian and upland habitats before harvest; 22 species were detected in riparian habitats and 26 were detected in upland habitats (Table 4). Species composition of the two habitats was very similar (Table 4). The probability of detecting a species was similar in both habitat types and was quite high (>85% for both habitat types; Table 4). No species was unique to the riparian habitat, but five species were unique to the upland habitat (Cedar Waxwing [*Bombycilla cedrorum*], Dark-eyed Junco [*Junco hyemalis*], Hermit × Townsend's Warbler [*Dendroica townsendi* × *D. occidentalis*], Band-tailed Pigeon [*Columba fasciata*], and Hermit Thrush [*Catharus guttatus*]).

Species group comparisons.—Neotropical migrants and residents were more abundant in riparian than in upland habitats (Table 5), and short-distance migrants were equally abundant in riparian and upland habitats (Table 5). Species associated with deciduous trees and shrubs in forested habitats were more abundant in riparian habitats than in the adjacent upland habitats (Table 5), and the abundance of species associated with conifer trees and shrubs in open habitats did not differ between riparian and upland habitats (Table 5). No spe-

TABLE 2. Habitat variables (mean, with 1 SE in parentheses) measured before timber harvest and after timber harvest along riparian and upland transects.

Habitat variable	Preharvest				Postharvest riparian	
	Riparian <i>n</i> = 18	Upland <i>n</i> = 18	<i>t</i>	<i>P</i>	Control <i>n</i> = 6	Wide <i>n</i> = 6
Canopy cover (%)	96.75 (0.46)	98.09 (0.32)	-2.48	0.02	94.76 (1.01)	65.86 (6.38)
Deciduous < 50 cm dbh (count)	71.56 (9.25)	30.50 (5.47)	3.26	0.00	56.29 (16.73)	69.33 (8.95)
Deciduous > 50 cm dbh (count)	1.39 (0.43)	0.50 (0.20)	1.93	0.06	4.71 (1.41)	3.83 (1.83)
Hemlock/cedar < 50 cm dbh (count)	75.67 (11.93)	99.72 (11.81)	-1.63	0.11	71.29 (17.45)	70.83 (15.44)
Hemlock/cedar > 50 cm dbh (count)	3.33 (0.96)	5.06 (1.86)	-0.49	0.63	13.86 (5.53)	2.67 (0.76)
Douglas-fir < 50 cm dbh (count)	18.11 (3.86)	50.28 (13.01)	-2.96	0.01	9.86 (1.30)	22.00 (14.66)
Douglas-fir > 50 cm dbh (count)	4.22 (0.92)	10.67 (1.91)	-2.93	0.01	9.29 (2.50)	4.83 (2.09)
Vine maple (count)	42.22 (6.87)	98.44 (28.66)	-0.43	0.67	32.57 (12.15)	33.50 (11.11)
Evergreen shrubs (%)	1.69 (1.07)	4.16 (1.60)	-1.75	0.09	0.31 (0.22)	0.64 (0.31)
Berry-producing shrubs (%)	37.90 (6.14)	10.83 (2.80)	4.08	0.00	31.52 (5.56)	27.58 (5.67)
Deciduous shrubs (%)	5.49 (1.45)	1.47 (0.54)	2.98	0.01	5.19 (2.14)	7.46 (4.33)
Snags (count)	24.11 (3.29)	39.61 (4.70)	-2.67	0.01	24.14 (5.27)	22.50 (2.71)
Logs (%)	26.56 (3.97)	27.30 (2.98)	-0.48	0.63	16.58 (5.26)	24.22 (2.13)
Buffer width (m)						30.52 (4.03)

Notes: Treatments include sites in unharvested controls (control), sites harvested with a wide riparian buffer (wide), and sites harvested with a narrow riparian buffer (narrow). We report *t* and *P* values from paired *t* tests comparing riparian and upland habitat variables before harvest, and two-sample *t* tests comparing upland habitat variables between the Wide and Narrow riparian buffer treatments postharvest.

† Value for the two-sample *t* test comparing buffer width between the two logging treatments postharvest.

cies group was more abundant in upland habitats (Table 5).

Abundance comparisons.—We detected 62 breeding bird species, representing 4646 observations, within the 15 m radius point-count stations during three years of observation. Before harvest, 86% of all detections in riparian and upland habitats were of five species: Chestnut-backed Chickadee (*Poecile rufescens*), Winter Wren (*Troglodytes troglodytes*), Pacific-slope Flycatcher (*Empidonax difficilis*), Golden-crowned Kinglet (*Regulus satrapa*), and Wilson's Warbler (*Wilsonia pusilla*). Total abundance was higher in riparian habitats (Table 5).

As with grouped species comparisons, no individual species was more abundant in the upland habitats in the preharvest year. However, the following species were rarely detected in the preharvest year and, when detected, they were found exclusively in the uplands: Cedar Waxwing, Dark-eyed Junco, and Hermit × Townsend's Warbler. Four species were more abundant in riparian than in upland habitats (Table 5): American Robin (*Turdus migratorius*), Black-throated Gray Warbler (*Dendroica nigrescens*), Pacific-slope Flycatcher, and Winter Wren. All four of these species demonstrated significant correlations with riparian habitat features; three were positively correlated with berry-producing shrubs and two were positively correlated with deciduous trees (Table 6).

Riparian and upland habitat features after harvest

Habitat variables measured along the riparian transect differed among treatments after harvest (Table 2; $F = 3.92$; $df = 26, 6$; $P = 0.05$). On treated sites, logging reduced the amount of canopy cover, the number of large hemlock/redcedar trees, and the percent

cover of berry-producing shrubs, and increased the percent cover of logs (Table 2). Mean buffer width differed between the narrow- and wide-buffer treatments (Table 2). The clear-cut uplands of the two treatments were similar (Table 2).

Effect of riparian buffer width on breeding bird community

Community comparisons.—The number of species on narrow-buffer sites increased from slightly fewer than controls before harvest to an average of 10 more species than controls after harvest (Fig. 1a). This change is reflected in an average increase of 20% in species turnover on narrow-buffer sites after harvest (Fig. 1b). Species richness and turnover were similar in the wide-buffer treatment and the control (Fig. 1b).

Species group comparisons.—Residents, short-distance migrants, cavity nesters, and species associated with conifer trees and shrubs in open habitats demonstrated a year × treatment interaction (Table 1). Univariate *F* tests indicated that residents and species associated with conifer trees were less abundant on the narrow-buffer than the wide-buffer treatment and control in 1996; short-distance migrants were more abundant on both treatments relative to the control in 1995 and 1996; species associated with shrubs in open habitats were more abundant on both treatments in 1996 (See Table 1 for univariate *F* and *P* values). We also examined the treatment effect for species groups not demonstrating a year × treatment interaction. We used univariate *F* tests for each year because of the low power associated with the interaction test (power < 0.30) for these species groups; species associated with shrubs in forested habitats were less abundant in the narrow-buffer than in the wide-buffer treatment and

TABLE 2. Extended.

Postharvest riparian			Postharvest upland			
Narrow <i>n</i> = 5	<i>F</i>	<i>P</i>	Wide <i>n</i> = 6	Narrow <i>n</i> = 5	<i>t</i>	<i>P</i>
35.70 (4.94)	55.60	0.00	6.29 (5.27)	0.33 (0.25)	1.13	0.33
37.00 (6.98)	1.09	0.36	16.17 (8.69)	12.40 (3.36)	0.41	0.70
4.0 (0.78)	0.30	0.74	0.17 (0.17)	0.0		
96.0 (18.19)	0.51	0.61	12.83 (8.92)	2.40 (0.98)	1.16	0.30
1.80 (0.66)	5.69	0.01	0.17 (0.17)	0.0		
7.00 (2.88)	0.95	0.41	13.83 (4.81)	3.20 (2.33)	1.99	0.09
4.80 (1.43)	0.79	0.47	0.50 (0.50)	0.0	0.34	0.74
33.20 (8.13)	0.19	0.83	6.50 (4.28)	29.20 (17.05)	-1.29	0.26
0.57 (0.22)	0.73	0.50	0.32 (0.14)	0.18 (0.07)	0.93	0.38
9.10 (5.21)	7.87	0.01	3.40 (1.68)	1.96 (1.05)	0.73	0.49
2.73 (1.07)	0.25	0.78	0.16 (0.09)	0.12 (0.06)	0.34	0.74
15.60 (2.77)	0.91	0.43	4.67 (1.33)	5.80 (1.66)	-0.53	0.61
33.46 (1.51)	6.10	0.01	19.22 (2.11)	23.45 (3.28)	-1.09	0.31
13.70 (2.65)	3.49†	0.01				

control in 1996 (Table 1). There was no difference in the abundance of any species group between treatments and controls in the preharvest year.

Abundance comparisons.—Total bird abundance did not demonstrate a year \times treatment interaction (Table 1). Five species demonstrated a year \times treatment effect (Table 1). Of these five species, only two showed a treatment effect in a given year: Black-throated Gray Warbler was less abundant on both treatments relative to controls in 1995 and was rarely detected in 1996; Song Sparrow (*Melospiza melodia*) was more abundant on the narrow-buffer treatment in 1996 (See Table 1 for univariate *F* and *P* values). Cedar Waxwing and Dark-eyed Junco were not detected in the preharvest year and, consequently, we did not expect a treatment \times year interaction. However, the Cedar Waxwing did not show a treatment effect, but demonstrated an interaction effect; it was more abundant on the narrow-buffer treatment in 1995 and was more abundant on the wide-buffer treatment in 1996. The Dark-eyed Junco showed a treatment effect ($F = 4.0$; $df = 2, 14$; $P = 0.04$) and was more abundant on the narrow-buffer treatment in 1995. We also examined the potential treatment effect in each year for species not demonstrating a year \times treatment interaction because of the low power associated with the interaction test (power < 0.30) for these species. In this univariate test, four species

showed a treatment effect in one or both years postharvest: Golden-crowned Kinglet was more abundant on controls than on treatments in both years postharvest; Wilson's Warbler (*Wilsonia pusilla*) was less abundant on the narrower treatment in 1995; Brown Creeper (*Certhia americana*) was more abundant on the control than on treatments in 1996; and Western Tanager (*Piranga ludoviciana*) was more abundant on the wide-buffer treatment in 1995. There was no difference in the abundance of any species between treatments and controls in the preharvest year.

Although buffer width was different between the two buffer treatments after harvest, there was overlap between the widest mean buffer width on the narrower treatment (range 7.3–23.2 m) and the narrowest mean buffer width on the wider treatment (range 20.6–47.9 m). Consequently, we compared mean species abundance in the two years postharvest with mean buffer width on logged sites after harvest. For this analysis, we used only the four species associated with riparian habitats. American Robin abundance increased on buffers after harvest, and there was a weak relationship with buffer width ($F = 4.57$; $df = 1, 9$; $r^2 = 0.37$, $P = 0.06$), indicating that this increase was greatest on the widest buffers. There was no relationship between Pacific-slope Flycatcher ($F = 1.61$; $df = 1, 9$; $P = 0.24$) and Winter Wren ($F = 0.82$; $df = 1, 9$; $P = 0.39$) abundance and buffer width. Black-throated Gray Warbler abundance was positively correlated with riparian buffer width ($F = 12.37$; $df = 1, 9$; $r^2 = 0.58$, $P = 0.007$); the number of Black-throated Gray Warbler detections decreased on eight of the 11 logged sites, didn't change on two, and increased on one (Fig. 2). This species was detected on six of the seven control sites postharvest. We determined recommended buffer widths for the Black-throated Gray Warbler by projecting the mean abundance value for controls after harvest onto the regression line in Fig. 2 (see *Methods*).

TABLE 3. Standardized correlations of four habitat variables with the discriminant axis for riparian and upland habitats.

Habitat variable	Correlation with canonical axis
Canopy cover	0.63
Deciduous < 50 cm dbh	-0.48
Evergreen shrubs	0.73
Douglas-fir > 50 cm dbh	0.69

Note: Positive values and variables are associated with upland habitats, and negative values and variables are associated with riparian habitats.

TABLE 4. Estimates of bird species richness, proportion of shared species, number of species unique to a habitat, and average species detection probability on riparian ($n = 18$) and adjacent upland ($n = 18$) habitats in coastal Washington State.

Parameter	Estimate	1 SE	95% CI
Riparian species richness	21.66	3.29	21.66–29.83
Upland species richness	25.89	1.90	22.00–27.89
Members of upland habitats present in the riparian habitats	19.94	2.02	16.94–23.89
Member of riparian habitats present in upland habitats	21.83	3.11	16.94–28.89
Proportion of upland habitat species present on riparian habitats	0.95	0.06	0.81–1.0
Proportion of riparian species present on upland habitats	0.99	0.07	0.75–1.0
Relative richness of riparian and upland habitats	1.20	0.12	0.80–1.24
No. species unique to upland habitats	5.32	2.20	0.00–7.5
No. species unique to riparian habitats	0.0	0.0	0.0
Detection probability in riparian habitat	0.97	0.08	0.70–0.97
Detection probability in upland habitat	0.85	0.07	0.79–1.0

Under this method, estimated buffer widths ranged from 45 to 65 m with a mean of 55 m.

DISCUSSION

Riparian and upland bird community before harvest

Riparian zones were characterized by deciduous trees and shrubs and berry-producing shrubs. In contrast, upland sites had higher canopy closure and more Douglas-fir trees and snags. Discriminant analysis successfully separated riparian and upland habitats 94% of the time, indicating that riparian zones had more of some habitat features than did the adjacent uplands. Despite these differences in vegetation characteristics between riparian and upland habitats, we found no differences in bird species richness and species composition between riparian and upland habitats. The high

tributary density in the uplands and the relatively wet, maritime climate of the coastal Pacific Northwest reduces moisture differences between upland and riparian habitats. Consequently, many of the habitat features found in riparian habitats are also found in the uplands, but to a lesser extent. Thus, unless species need extensive riparian habitat, they should also be found in the uplands.

The uplands contained more Douglas-fir trees, which are indicative of drier conditions. Consequently, we would expect some bird species to be adapted to this relatively dry, upland habitat condition. This may explain why McGarigal and McComb (1992) found species richness to be higher and the abundance of five species to be greater in the uplands than in riparian habitats of the Oregon Coast range. Although we found

TABLE 5. Detection rate (mean \pm 1 SE) in riparian and upland habitats, before harvest, of common species and species grouped according to migratory pattern and habitat use.

Species and species groups	Preharvest 1993		<i>t</i>	<i>P</i>
	Riparian <i>n</i> = 18	Upland <i>n</i> = 18		
Individual species				
Chestnut-backed Chickadee	3.21 (1.32)	3.20 (1.23)	0.03	0.97
Winter Wren	3.05 (1.03)	1.26 (0.62)	6.32	0.00
Pacific-slope Flycatcher	1.94 (0.55)	1.21 (0.66)	3.60	0.00
Golden-crowned Kinglet	1.03 (0.73)	1.37 (0.98)	-1.20	0.24
Wilson's Warbler	0.57 (0.74)	0.43 (0.61)	0.63	0.54
Swainson's Thrush	0.21 (0.29)	0.23 (0.35)	-0.21	0.84
Brown Creeper	0.16 (0.18)	0.24 (0.22)	-1.28	0.21
Black-throated Gray Warbler	0.25 (0.26)	0.09 (0.11)	2.38	0.02
American Robin	0.18 (0.31)	0.02 (0.07)	2.06	0.05
Mean abundance/site	10.79 (0.53)	8.48 (0.63)	2.81	0.01
Species groups				
Neotropical migrants	3.12 (0.34)	2.25 (0.27)	2.02	0.05
Short-distance migrants	0.19 (0.08)	0.14 (0.04)	0.52	0.61
Residents	7.48 (0.32)	6.09 (0.48)	2.41	0.02
Conifer trees	4.39 (0.40)	4.94 (0.51)	-0.85	0.40
Deciduous trees	2.37 (0.21)	1.33 (0.16)	3.97	0.00
Shrubs in open habitats	0.03 (0.02)	0.04 (0.03)	-0.31	0.76
Shrubs in forested habitats	3.62 (0.31)	1.68 (0.22)	5.05	0.00

Note: Values of *t* and *P* are given for the comparison of riparian vs. upland habitats before harvest.

TABLE 6. Relationship between riparian-associated species abundance and habitat variables (Table 2) in the preharvest year (1993 in coastal Washington State).

Species	Berry-producing shrubs	Deciduous < 50 cm dbh	Deciduous > 50 cm dbh	Douglasfir < 50 cm dbh	r^2	$F_{2,33}$	P
American Robin	0.49				0.24	10.76	0.002
Black-throated Gray Warbler			0.62		0.38	20.9	<0.001
Pacific-slope Flycatcher	0.46			-0.36	0.31	7.30	0.002
Winter Wren	0.38	0.37			0.40	10.93	<0.001

Note: Values are standardized correlation coefficients for each habitat variable included in the model and overall r^2 , F , and P values.

no difference in species richness between riparian and upland habitats, five species appear to be unique to upland habitats (Table 4). In addition, several species (Brown Creeper [*Certhia americana*], Golden-crowned Kinglet [*Regulus satrapa*], Hermit \times Townsend's Warbler [*Dendroica townsendi* \times *D. occidentalis*], and Dark-eyed Junco [*Junco hyemalis*]) appear to be more abundant in the uplands and may show significant trends with larger sample sizes.

Total abundance and the abundance of several species and species groups were higher in riparian habitats

than in adjacent uplands. Riparian zones are typically more structurally diverse and more productive than the adjacent uplands (Bull 1978), and therefore may be able to support higher densities of birds. Higher total abundance in riparian habitats can be explained by the abundance patterns of the four riparian-associated species (American Robin [*Turdus migratorius*], Pacific-slope Flycatcher [*Empidonax difficilis*], Black-throated Gray Warbler [*Dendroica nigrescens*], and Winter Wren [*Troglodytes troglodytes*]). The abundance of these species is correlated with habitat features more common to riparian zones, such as deciduous trees and berry-producing shrubs. The Winter Wren is more abundant along streams in Oregon (McGarigal and McComb 1992) and British Columbia (Kinley and Newhouse 1997), and is probably using riparian habitats because they have a greater cover of deciduous shrubs (Barrows 1986). The Black-throated Gray Warbler is associated with deciduous tree cover in Oregon (Morrison 1982), and is probably selecting riparian habitats because of their greater cover of red alder and big-leaf maple. The Pacific-slope Flycatcher frequently builds its nest behind adventitious branches on red alder trees (S. F. Pearson and M. Leu, unpublished data), which are more common in riparian habitats. The American Robin is associated with riparian habitats in British Columbia (Wiebe and Martin 1998), and it may find preferable habitat for foraging and nesting in the deciduous tree- and shrub-dominated riparian habitats. Berry-producing shrubs may be an important habitat feature for the American Robin, which is highly frugivorous (Malmborg and Willson 1988, Parrish 1997).

Effect of buffer width on the breeding bird community

Species turnover was higher on the narrow-buffer treatment than on the wide-buffer treatment and controls. Resident species and species associated with conifer trees and shrubs in forested habitats also declined on the narrow-buffer treatment. Interior forest species (Brown Creeper; McGarigal and McComb 1995), conifer forest species (Golden-crowned Kinglet; Mannan and Meslow 1984), and riparian forest species (Black-throated Gray Warbler; this study) declined on both buffer treatments. Short-distance migrants and species associated with shrubs and open habitats (Dark-eyed

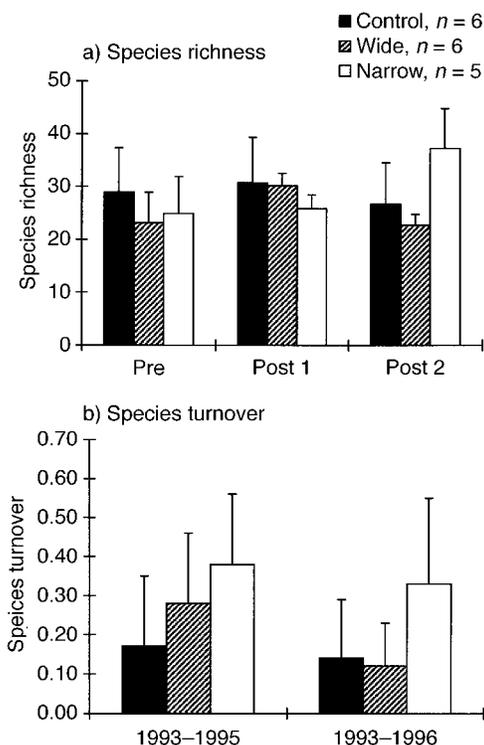


FIG. 1. (a) Bird species richness in the preharvest year (Pre) and the first (Post 1) and second (Post 2) years after harvest in three types of riparian habitat: not harvested (control), harvested with a wide riparian buffer (wide), or harvested with a narrow riparian buffer (narrow). (b) Species turnover between the preharvest year and the first year after harvest (1993-1995) and between the preharvest year and the second year after harvest (1993-1996) in the control and buffer treatments. Values are depicted as means + 1 SE.

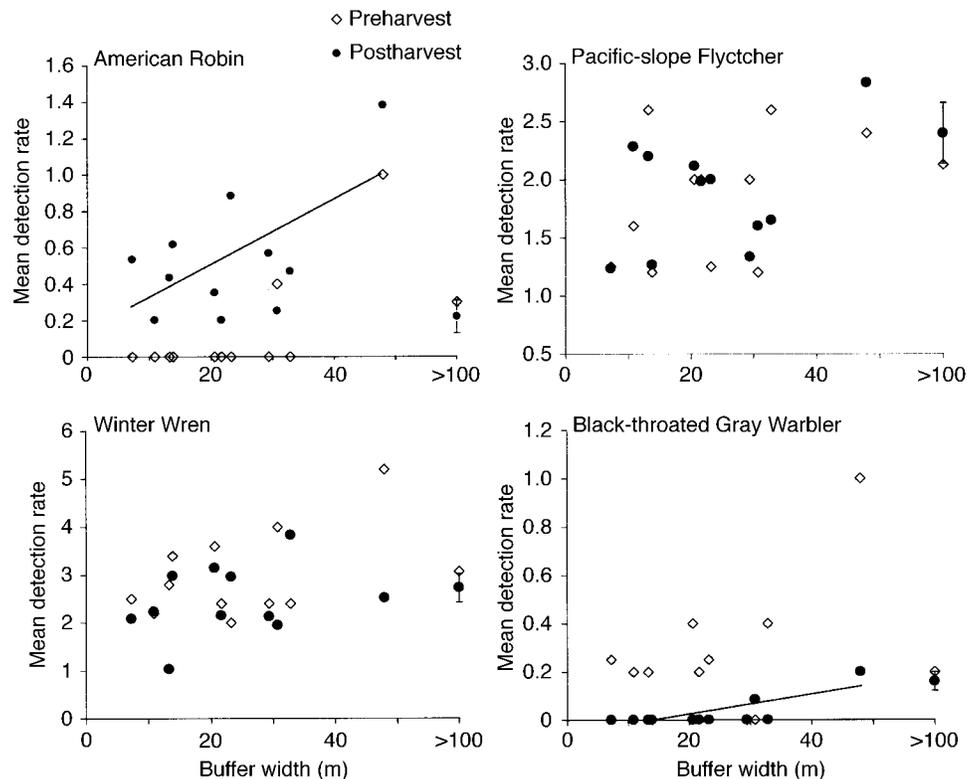


FIG. 2. Relationship between riparian buffer width and mean detection rate for the four riparian-associated species in the preharvest year and in the two postharvest years combined. The two points directly above the buffer width ">100" represent the mean (± 1 SE) detection rate for all six controls in the preharvest year and all six controls in the two years postharvest combined. All other data points represent the mean detection rate per site. Regression lines for Black-throated Gray Warbler and American Robin were derived using the mean detection rate on logged sites in the two years postharvest.

Junco, Song Sparrow [*Melospiza melodia*], and Cedar Waxwing [*Bombycilla cedrorum*]; Morrison and Mellow 1983) increased on treated sites, particularly on the narrow-buffer treatment.

These postharvest changes in the riparian bird community may be the result of several factors. First, the elongated shape of riparian zones creates a high ratio of edge : area. Thus, forest interior species and species sensitive to fragmentation are likely to decline in these habitats (e.g., Black-throated Gray Warbler and Brown Creeper; Rosenberg and Raphael 1986, McGarigal and McComb 1995). Conversely, species associated with edge and more open habitats are likely to increase in abundance (e.g., Dark-eyed Junco and Song Sparrow). Second, harvesting the upland habitats decreases the amount of conifer forest in the riparian buffer disproportionately. This occurs because deciduous trees are largely confined to a narrow strip along the stream edge and conifers dominate the uplands. The low proportion of conifer trees remaining in the narrow-buffer strips may explain why we found conifer associates to decline on the narrowest riparian buffers. Third, timber harvest within the riparian zone changes the amount of light penetration and the microclimatic regime (Brosofske et al. 1997) and, consequently, the vegetation and crit-

ical food resources such as insects. Finally, the nature of the adjacent upland vegetation may also influence the riparian community (Szaro and Jakle 1985). In our study, the vegetation characteristics of the clear-cut uplands of both buffer treatments were similar and thus should influence both buffer treatments similarly. However, as the uplands succeed into young conifer stands, the vegetation and climatic changes caused by logging will become less pronounced.

Scope and limitations

There are several limitations to our study that should be considered before applying these results to management prescriptions, and that highlight the need for additional research. We describe short-term effects of our buffer treatments on the bird community. However, the breeding bird community may take several years to respond to habitat manipulations (Wiens et al. 1986, Darveau et al. 1995, Hagan et al. 1996). There is evidence that birds will "pack" into the forested riparian buffer in the year after clearcutting and then decline in the following years (Darveau et al. 1995). This pattern of "packing" appears to be caused by strong philopatry of territorial males. We found no evidence that birds were "packing" into the forested buffers in the

first year after harvest, or of a decline after harvest; total bird abundance was similar among treatments and controls in all three years. However, it may take more than two years for bird abundance to respond to treatment effects. Change in bird abundance and species composition over time may be the result not only of bird community relaxation but also of vegetation changes (e.g., regeneration and tree blowdown). Thus, we recommend censusing these sites again 5 yr and 10 yr postharvest to document longer term effects of harvest on the bird and plant community.

Small-radius point counts resulted in small sample sizes for many species and, consequently, several of our statistical tests had low power. In addition, the relatively small amount of area sampled by our point counts (~10% of the area represented by a 15 m wide \times 500 m long buffer) increased the potential for sampling error. Thus, some of the species groups and individual species that did not demonstrate a treatment effect in our study may actually be sensitive to riparian buffer width. For example, both the Pacific-slope Flycatcher and Winter Wren were nearly twice as abundant on controls than on the narrow-buffer treatment in the second year after harvest, yet we did not detect a treatment effect. Hagar (1999) found these two riparian associates to be absent from riparian buffers <18 m wide, and that their abundance on buffers narrower than 80 m was lower than the average for unlogged sites. Hagar's results, coupled with our low statistical power, suggest that these species may actually be sensitive to riparian buffer width. Thus, in order to increase sample sizes and statistical power, we recommend that researchers use strip transects or territorial mapping, even in extremely steep and rugged terrain.

Point counts or spot mapping do not adequately census species that occur at low densities, that do not defend territories using song or other audible displays, or that range widely during the breeding season (e.g., Pileated Woodpecker [*Dryocopus pileatus*], raptors, grouse, waterfowl, and shorebirds). Determining the importance of riparian zones to these species may require more intensive autecological studies.

Riparian buffers may serve many critical biological functions not examined by this study. They may serve as corridors connecting forest patches and, consequently, they may facilitate genetic and ecological exchange between patches (Noss 1983, Gregory et al. 1991, Machtans et al. 1996, Schmiegelow et al. 1997). For example, Machtans et al. (1996) examined the potential role of riparian buffer strips as corridors and found them to be important to natal bird dispersal.

It is unclear what potential fitness costs might be associated with confining birds to narrow, linear riparian strips of potential habitat. Many territorial passerines have territories that are 3–30 ha in size and often irregular in shape. Thus, confining birds to narrow, linear riparian strips after timber harvest is likely to change territory shape and position for some species.

Change in territory shape could reduce the territory holder's fitness by depleting potential food resources, increasing intra- and interspecific competition, and reducing pairing and nesting success (Lambert and Hannon 2000). Lambert and Hannon (2000) studied Ovenbirds (*Seiurus aurocapillus*) in riparian buffers 20, 100, and 200 m wide in Alberta, Canada. Ovenbirds were absent from 20-m buffers and they shifted their territory position lakeward after logging occurred in 100-m buffers; however, territory size and pairing success were not changed in the 100-m buffer when compared with controls. The effects of changing the territory size and shape of riparian-associated species need to be examined before we can evaluate the potential fitness costs of confining bird territories to narrow strips of riparian habitat after clearcutting the adjacent uplands.

Management implications

Differences in habitat characteristics and bird communities between riparian and upland habitats suggest the need for maintaining riparian reserves along streams. High species turnover on the narrow-buffer treatment indicates that riparian buffers <14 m on each side of second- and third-order streams do not maintain the pre-logging bird community. There was little difference in species turnover or species richness between the wide-buffer treatment and the control, indicating that a 30-m buffer on both sides of second- and third-order streams maintains most of the pre-logging bird community in the first two years after harvest.

Abundance of all four riparian associates was correlated with percent cover of berry-producing shrubs or numbers of deciduous trees. Within the riparian zone, red alder and big-leaf maple were the predominant deciduous tree species, whereas salmonberry (*Rubus spectabilis*) and huckleberry (*Vaccinium* sp.) were the predominant berry-producing shrubs. Thus, we recommend maintaining these important riparian habitat features within forested riparian buffers. The deciduous tree component may be vulnerable to blowdown in the narrow-buffer treatment after logging (*personal observation*), suggesting the need to maintain wider buffers in areas prone to high winds.

The wide-buffer treatment did not maintain the Black-throated Gray Warbler, Brown Creeper, and Golden-crowned Kinglet as well as did controls, indicating that a 30-m buffer may not be wide enough to maintain the entire pre-logging bird community. Our regression of buffer width vs. species abundance indicates that the Black-throated Gray Warbler was not found in riparian buffers narrower than 30 m per side and reached abundance levels comparable to those found on controls in buffer strips 45–65 m in width. However, because our widest buffer was ~48 m, we do not feel comfortable projecting the potential population impacts of buffers wider than those used in our study. Thus, we recommend 45 m as a very conser-

vative minimum forested buffer required to maintain the entire pre-logging bird community along second- and third-order streams in the Pacific Northwest in the short term.

Rosenberg and Raphael (1986) found the abundance of the Black-throated Gray Warbler to be positively correlated with stand area. Our results suggest that this species may be sensitive to forest fragmentation or that it requires larger buffers because it uses attributes of both the riparian and upland community. Most of the deciduous trees on our sites (with which the Black-throated Gray Warbler is closely associated) occur within a narrow streamside strip and are likely to be completely contained in a buffer <30 m, yet this warbler was only found in buffers >30 m wide. A reexamination of our vegetation data indicates that the number of red alder trees within 8 m of the stream was greater than the number 8–16 m from the stream ($P = 0.002$); the number of Douglas-fir trees within 8 m of the stream was less than the number 8–16 m from the stream ($P = 0.002$).

Our recommended 45-m riparian buffer appears to agree with the buffer width recommended by Hagar (1999) for streams in western Oregon. Hagar (1999) identified eight forest-associated species (including Brown Creeper and Golden-crowned Kinglet) that appeared to be more abundant or detected only in unlogged riparian buffers. She recommended riparian buffers >40 m wide on each side of the stream to provide the greatest benefit for forest-associated bird species. However, she found the abundance of four species to be less in buffers narrower than 70 m than in unlogged controls. Darveau et al. (1995), working in the boreal forest of Quebec, found that forested riparian buffers 20 and 40 m wide did not maintain abundances of forest-dwelling species, but buffers 60 m wide supported a bird community similar to that of unharvested controls. Kinley and Newhouse (1997), examining breeding bird characteristics among riparian buffers 70, 37, and 14 m wide in southeastern British Columbia, found that the density of riparian-associated species increased with increasing buffer width, but that species diversity and equitability did not differ among treatments. These studies suggest that the minimum buffer width necessary for maintaining the pre-logging bird community differs regionally, and may be influenced by local species composition and ecological conditions.

ACKNOWLEDGMENTS

For field assistance, we thank Grant Canterbury, John Frisch, Neil Fergusson, Peter Gibert, Paul Hendig, Dave Meade, Mark Moon, Jennifer Pretare, and Richard Young. The manuscript was improved by the comments of Susan Hannon, Kathryn Kelsey, John Kilgo, Matthias Leu, Cheryl Quade, and two anonymous reviewers. We are especially thankful to Kathryn Kelsey for overseeing the vegetation measurements and numerous other aspects of this study. We thank Champion Pacific Timberlands, City of Seattle, International Paper, Hampton Tree Farms, Plum Creek Timber, The Weyerhaeuser Company, and Washington State Department of Natural Resources

for providing study sites and logistical support. We thank Washington Forest Protection Association, Washington Hardwoods Commission, The Weyerhaeuser Company, and Plum Creek Timber for financial support in 1993 and 1995. We thank the Washington Department of Natural Resources and the Timber Fish and Wildlife members for funding and logistical support throughout.

LITERATURE CITED

- Barrows, C. W. 1986. Habitat relationships of winter wrens in northern California. *Western Birds* **17**:17–20.
- Brososke, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications* **7**:1188–1200.
- Bull, E. L. 1978. Specialized habitat requirements of birds: snag management, old growth, and riparian habitat. Pages 74–82 in R. M. DeGraaf, technical coordinator. Proceedings of the Workshop on Nongame Bird Habitat Management in the Coniferous Forests of the Western United States. U.S. Forest Service General Technical Report **PNW-64**.
- Bull, E. L., and J. W. Skovlin. 1982. Relationships between avifauna and streamside vegetation. Transactions of the North American Wildlife and Natural Resource Conference **47**:496–506.
- Carey, A. B., M. M. Hardt, S. P. Horton, and B. L. Biswell. 1991. Spring bird communities in the Oregon Coast Range. Pages 123–142 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Forest Service General Technical Report **PNW-285**.
- Darveau, M., P. Beauchesne, L. Bélandger, J. Huot, and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. *Journal of Wildlife Management* **59**:67–78.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.
- Gilbert, F. G., and R. Allwine. 1991. Spring bird communities in the Oregon Cascade Range. Pages 145–158 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Forest Service General Technical Report **PNW-285**.
- Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. *American Midland Naturalist* **129**:288–300.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* **41**:540–551.
- Hagan, J. M., III, W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* **10**:188–202.
- Hagar, J. C. 1999. Influence of riparian buffer width on bird assemblages in western Oregon. *Journal of Wildlife Management* **63**:484–496.
- Hines, J. E., T. Boulinier, J. D. Nichols, J. R. Saurer, and K. H. Pollock. 1999. COMDYN: software to study the dynamics of animal communities using a capture–recapture approach. *Bird Study* **46**:S209–217.
- Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert Stream. *Ecology* **67**:629–638.
- Johnson, R. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: a concept. Pages 68–97 in R. R. Johnson and D. A. Jones, technical coordinators. Importance, preservation and management of riparian habitat: a symposium. U.S. Forest Service General Technical Report **RM-166**.
- Kilgo, J. C., R. A. Sargent, B. R. Chapman, and K. V. Miller.

1998. Effect of stand width and adjacent habitat on breeding bird communities in bottomland hardwoods. *Journal of Wildlife Management* **62**:72–83.
- Kinley, T., and N. J. Newhouse. 1997. Relationship of riparian reserve zone width to bird density and diversity in southeastern British Columbia. *Northwest Science* **71**:75–86.
- Knopf, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105–111 in R. R. Johnson, C. D. Ziebell, D. R. Patten, P. F. Ffolliot, and R. H. Hamre, technical coordinators. *Riparian ecosystems and their management: reconciling conflicting uses*. U.S. Forest Service General Technical Report **RM-120**.
- Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* **100**:272–284.
- Lambert, J. D., and S. J. Hannon. 2000. Short-term effects of upland timber harvest on Ovenbird abundance, territory characteristics, and pairing success in riparian buffer strips. *Auk* **117**:687–698.
- Lemmon, P. E. 1957. A new instrument for measuring forest overstory cover. *Journal of Forestry* **55**:667–668.
- Machtans, C. S., M. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* **10**:1366–1379.
- Malmborg, P. K., and M. F. Willson. 1988. Foraging ecology of avian frugivores and some consequences from seed dispersal in an Illinois woodlot. *Condor* **90**:173–186.
- Mannan, R. W., E. C. Meslow. 1984. Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. *Journal of Wildlife Management* **48**:1219–1238.
- Manuwal, D. A. 1991. Spring bird communities in the southern Washington Cascade Range. Pages 161–174 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Forest Service General Technical Report **PNW-285**.
- Manuwal, D. A., and S. F. Pearson. 1997. Bird populations in managed forests in the western Cascade Mountains, Washington. Pages 1–61 in K. B. Aubry, S. D. West, D. A. Manuwal, A. B. Stringer, J. L. Erickson, and S. F. Pearson, editors. *Wildlife use of managed forests: a landscape perspective*. Timber Fish and Wildlife Technical Report **TFW-WL4-98-002**.
- McGarigal, K., and W. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. *Journal of Wildlife Management* **56**:10–23.
- McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* **65**:235–260.
- Morrison, M. L. 1982. The structure of western warbler assemblages: ecomorphological analysis of the Black-throated Gray and Hermit Warblers. *Auk* **99**:503–513.
- Morrison, M. L., and E. C. Meslow. 1983. Avifauna associated with early growth vegetation on clearcuts in the Oregon Coast Ranges. U.S. Forest Service Research Paper **PNW-305**.
- Murray, N. L., and D. F. Stauffer. 1995. Nongame bird use of habitat in central Appalachian riparian forests. *Journal of Wildlife Management* **59**:78–88.
- Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998a. Estimating rates of local species extinction, colonization, and turnover in animal communities. *Ecological Applications* **8**:1213–1225.
- Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998b. Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology* **12**:1390–1398.
- Noss, R. F. 1983. A regional approach to maintain diversity. *BioScience* **33**:700–706.
- Oakley, A. L., J. A. Collins, L. B. Everson, D. A. Heller, J. C. Howerton, and R. E. Vincent. 1985. Riparian zones and freshwater wetlands. Pages 57–80 in E. R. Brown, technical editor. *Management of wildlife and fish habitats in forests of western Oregon and Washington*. U.S. Department of Agriculture **R6-F & WL-192-1985**.
- Parrish, J. D. 1997. Patterns of frugivory and energetic condition in Nearctic land birds during autumn migration. *Condor* **99**:681–697.
- Rosenberg, K. V., and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263–272 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:18–32.
- Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**:1914–1932.
- Spackman, S. C., and J. W. Hughes. 1995. Assessment of minimum stream corridor width for biological conservation: species richness and distribution along mid-order streams in Vermont, USA. *Biological Conservation* **71**:325–332.
- Stauffer, D. I. and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. *Journal of Wildlife Management* **44**:1–15.
- Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. *American Geophysical Union Transactions* **38**:913–920.
- Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *BioScience* **38**:92–98.
- Szaro, R. C., and M. D. Jakle. 1985. Avian use of a desert riparian island and its adjacent scrub habitat. *Condor* **87**:511–519.
- Thomas, J. W., C. Maser, and J. E. Rodiek. 1979. Riparian zones. Pages 40–47 in J. W. Thomas, technical editor. *Wildlife habitats in managed forest: the Blue Mountains of Oregon and Washington*. U.S. Forest Service Handbook Number 553, Washington, D.C., USA.
- Verner, J. 1985. Assessment of counting techniques. *Current Ornithology* **2**:247–302.
- Washington State Forest Practices Board. 1992. *Washington forest practices rules and regulations*. Olympia, Washington, USA.
- Welsh, D. A., and S. C. Lougheed. 1996. Relationships between bird community structure and species distributions to two environmental gradients in the northern boreal forest. *Ecography* **19**:194–208.
- Whitaker, D. M., and W. A. Montevecchi. 1999. Breeding bird assemblages inhabiting riparian buffer strips in Newfoundland, Canada. *Journal of Wildlife Management* **63**:167–179.
- Wiebe, K. L., and K. Martin. 1998. Seasonal use by birds of stream-side riparian habitat in coniferous forest of north-central British Columbia. *Ecography* **21**:124–134.
- Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. *Ecology* **67**:365–376.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* **125**:879–887.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.