
Effects of Patch Size on Birds in Old-Growth Montane Forests

JIM SCHIECK,*‡ KEN LERTZMAN,* BRIAN NYBERG,† AND RICK PAGE†

*Resource And Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

†Research Branch, Ministry of Forests, 31 Bastion Square, Victoria, British Columbia V8W 3E7, Canada

Abstract: *Following habitat alteration or fragmentation, competition, parasitism, and predation from species that live in the new habitats may reduce the survival and reproductive success of species living in the original habitats. Negative influences from species that live outside the remnant patches are expected to be greater in small rather than in large remnant patches because more "external" species are expected to move through the centers of small remnant patches. We surveyed birds within remnant patches of old-growth montane forests on Vancouver Island, Canada, (1) to evaluate whether the richness and abundance of non-old-growth bird species were larger at the center of small rather than large patches and (2) to evaluate whether the opposite was true of old-growth bird species. More non-old-growth bird species were present at the center of small remnant patches of old growth than in large old-growth patches. We found no relationship, however, between patch size and richness or abundance of old-growth bird species at the center of remnant patches of old growth. This was true for old-growth species with open, cup-shaped nests and cavity nests. Old-growth birds may have been affected less in our study area than in other areas because they evolved within heterogeneous montane forests and interacted with non-old-growth species throughout their evolutionary histories or because the contrast between old-growth forests and logged areas was less than that between the forests and agricultural/urban areas that were surveyed in other studies.*

Efectos del tamaño de parches sobre las aves en bosques primarios de montaña

Resumen: *Luego de la alteración o fragmentación del hábitat, la competencia, parasitismo y predación de especies que viven en los nuevos hábitats pueden reducir la supervivencia y el éxito reproductivo de las especies que viven en sus hábitats originales. Se espera que las influencias negativas por parte de las especies que viven fuera de los parches remanentes, será mayor en los parches pequeños que en los grandes, dado que se espera que una mayor cantidad de especies "externas" se traslade a través de los centros de los pequeños parches remanentes. Estudiamos pájaros dentro de los parches remanentes de los bosques primarios de montaña en la Isla de Vancouver, Canadá, para (1) evaluar si la riqueza y abundancia de especies de pájaros en los bosques no-primarios fue mayor en el centro de los parches pequeños que en el centro de los grandes y (2) evaluar si ocurría lo opuesto con las especies de pájaros de los bosques primarios. Una mayor cantidad de especies de pájaros de bosques no-primarios, estuvieron presentes en el centro de los parches remanentes pequeños de los bosques primarios que en los parches de mayor tamaño. Sin embargo, no encontramos relación alguna entre el tamaño del parche y la riqueza o abundancia de las especies de pájaros de bosques primarios en el centro de los parches remanentes en los bosques primarios. Esta situación se observó para las especies de bosques primarios con nidos abiertos en forma de taza y nidos en cavidades. Los pájaros de los bosques primarios podrían haber sido menos afectados en nuestra área de estudio en comparación con otras áreas, porque evolucionaron dentro de bosques montañosos heterogéneos e interactuaron con especies de crecimiento no-primario a través de sus historias evolutivas o por que el contraste entre bosques primarios y áreas taladas es menor que entre bosques y áreas agrícolas urbanas que han sido consideradas en otros estudios.*

‡ Current address: Wildlife Ecology Branch, Alberta Environmental Centre, Vegreville, Alberta, T9C 1T4, Canada
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Introduction

When an area is disturbed by humans (through mineral extraction, logging, agriculture, or urban development), new habitats are created. Concomitant with creation of the new habitats, some of the original habitats are lost and the remainder become fragmented (Burdick et al. 1989; Saunders 1989; Laurance & Yensen 1991). Populations of native vertebrates may be reduced by habitat changes if the new habitats are less suitable than the original habitats (Saunders et al. 1991). As a complicating factor, the communities within the newly created habitats may be different from those in the original habitats, and species living in the new habitats may invade the residual patches to prey upon (Saunders 1990; Yahner & DeLong 1992; Paton 1994), parasitize (Gates & Gysel 1978; Usher 1988), or compete with (Pahl et al. 1988; da Fonseca & Robinson 1990) native species.

Small patches have a greater proportion of edge than do large patches of the same shape; consequently, individuals that live within small patches may interact with species from the external communities to a greater extent than individuals living within large patches (Usher 1988). This may result in greater negative effects on native species within small patches than within large patches. In many previous studies, some native species had lower densities in small patches (Askins et al. 1990), and some native species were not present in small patches (Saunders 1990). Positive relationships between patch size and species presence or abundance have been used as evidence that large areas of nonfragmented habitat must be preserved if we wish to maintain all native vertebrates (Saunders et al. 1991; Wenny et al. 1993; Villard et al. 1993).

Although it is common for native species to be affected detrimentally by fragmentation and human development, this pattern may not be universal. To the extent that habitats created by humans are similar to those created by natural processes, communities within the altered landscapes may be similar to natural communities, and native vertebrates that live within remnant patches may be able to cope with the changes (Hansen et al. 1991; Rudnicki & Hunter 1993). In addition, if species have evolved in naturally heterogeneous landscapes, they may have evolved strategies to cope with diverse communities like those that accompany human-imposed fragmentation (Hansson & Angelstram 1991). For these reasons, the fragmentation paradigm may have limited applicability to some forested landscapes that are being managed for timber.

We surveyed bird communities at the center of remnant patches (patches that remain after the rest of the area has been logged) of old-growth (greater than 300 years old), coastal, temperate forest of western North America to determine whether richness and abundance of non-old-growth bird species (species that,

based on previous studies, have equal or higher abundance outside old-growth forest than they have within old-growth forest) were greater at the center of small rather than large remnant patches of old-growth forest. We also tested whether the richness and abundance of old-growth bird species (species that, based on previous studies, have higher abundance within old-growth forest than they have in other habitats) at the center of remnant patches of old-growth forest were positively related to patch size. Negative impacts of non-old-growth birds were hypothesized to have been strongest on old-growth birds that build open cup-shaped nests because predation of eggs should be more common from cup-shaped nests than from cavity nests (Wilcove 1985). In addition, if Brown-headed Cowbirds (*Molothrus ater*) are present outside the remnant patches, they may have parasitized species using cup-shaped nests (Paton 1994). Therefore, we also tested whether relationships differed between old-growth species with open cup-shaped nest and those with cavity nests.

Methods

Study Area

Using satellite images of Vancouver Island, Canada, we selected two areas (the Nimpkish River valley, 50°10'N, 126°30'W, and the plateau above Shawnigan Lake, 48°40'N, 124°0'W) with many remnant patches of old-growth forests. Both areas were in the mountains with an altitudinal range of approximately 1500 m and an abundance of small streams, rivers, and lakes. Forests in the areas varied from those dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) in dry areas to those dominated by western hemlock, amabilis fir (*Abies amabilis*), and western redcedar (*Thuja plicata*) in moist areas (Meidinger & Pojar 1991). As in other montane areas (Hansen et al. 1991), moist areas, riparian zones, and localized wind events had created abundant spatial heterogeneity in the forests prior to logging. Natural fires, although relatively infrequent on the study areas, resulted in most of both of the areas burning at least once during the past 1000 years (unpublished fire-history maps produced by forest companies).

During the past 100 years, forests on these two study areas were harvested by clear-cut logging. The amount of area harvested increased greatly during the last 40 years (unpublished forest harvesting maps). Within the Nimpkish River valley study area, logging was concentrated along the valley bottom; more than 80% of the old-growth forests on the valley bottom have been harvested, whereas less than 20% of forests at higher elevations have been harvested. Topographical relief and harvesting patterns within that area, however, show that all remnant patches of forest were within 2 km of large

tracts of unharvested forest. On the Shawnigan Plateau study area, approximately 70% of the original forests has been harvested, and some of the remnant patches were more than 4 km from large tracts of unharvested forests.

Prior to the 1950s many of the logged areas were allowed to regenerate naturally. Within the last 40 years, however, all areas that were logged were replanted with Douglas-fir, although western hemlock and western red cedar were planted on some of the moist sites. Until the mid 1980s much of the slash and organic debris that remained on the ground subsequent to logging was burned. Post-logging slash burns have become uncommon during the last five years.

Based on existing forest inventory from the forest companies in the two areas, we classified each remnant patch as old growth (more than 300 years old) or as younger forest. Only remnant patches larger than 4 ha and classified as old growth were considered candidates for this study. In addition, a potential remnant patch for this study had to be surrounded by logged areas that were at least 250 m wide. A few large forest birds (such as the Pileated Woodpecker, *Dryocopus pileatus*) may forage more than 250 m from their nest site (Bull & Holthausen 1993), but most birds do not travel that far. By having a 250 m buffer of logged forest, few of the birds that we detect within the remnant patches would have been living in other areas of old-growth forest. Remnant patches that had been isolated for less than five years were not surveyed because the dynamics of vertebrates living within the remnant patches may change greatly within the first few years (Lovejoy et al. 1986; Lehmkuhl et al. 1991). Finally, remnant patches adjacent to regenerating forests more than 35 years old were not included as potential patches because we wished to maximize the contrast between remnant patches and regenerating forests.

We determined the aspect and elevation of remnant patches and the number of live trees and snags greater than 50 cm within two 0.1-ha plots. We grouped remnant patches based on data from this initial survey and

found that only three habitat types/geographic areas were represented by at least five remnant patches and had a reasonable range of patch sizes. In the Nimpkish River valley there were 10 remnant patches of old-growth forest dominated by Douglas-fir and western hemlock, with patch size ranging from 4 to 500 ha. This group of remnant patches was labeled "Nimpkish-fir" (see Table 1 for descriptions of the habitat types/geographic areas). In addition, in the Nimpkish River valley we found five remnant patches of old-growth forest dominated by western hemlock, western red cedar, and amabilis fir ranging in size from 20 to 2500 ha (Nimpkish-hemlock patches). On the Shawnigan Plateau there were eight remnant patches of old-growth forests dominated by western hemlock and western red cedar ranging in size from 4 to 360 ha (Shawnigan-hemlock patches). We restricted subsequent surveys to these 23 remnant patches.

Bird Surveys

We used aerial photographs to position two survey stations near the center of each patch, such that the stations were separated by a distance of at least 200 m and were as far as possible from the edge of the patch. In the four smallest remnant patches (two Nimpkish-fir and two Shawnigan-hemlock), it was not possible to have two points 200 m apart and also a minimum of 100 meters from the edge of the patch. To obtain equal sampling effort in all patch sizes, it was necessary to pair patches that were smaller than 6 ha and to survey each member of the pair with half the intensity (at one station rather than two) of that used for larger patches. For those "pairs" of small patches, we analyzed data as if they were obtained in one patch, and we used the mean patch size for the pair. Consequently, sample size in all analyses was nine, five, and seven for the Nimpkish-fir, Nimpkish-hemlock, and Shawnigan-hemlock, respectively. Finding the center of largest two patches was difficult because topographical relief and wind events cre-

Table 1. Physical and vegetative characteristics (mean \pm SE) of three habitat types/geographic areas on Vancouver Island, Canada.

Characteristic	Nimpkish-Fir	Nimpkish-Hemlock	Shawnigan-Hemlock
Slope ($^{\circ}$)	21.1 \pm 5.2	35.4 \pm 5.6	31.0 \pm 5.8
Aspect ($^{\circ}$)	195 \pm 36	326 \pm 39	188 \pm 42
Elevation (m)	294 \pm 42	568 \pm 57	713 \pm 34
Douglas-fir (number stems > 50 cm/ha)	74.4 \pm 21.2	6.0 \pm 4.9	5.0 \pm 2.7
Western Hemlock (number stems > 50 cm/ha)	40.6 \pm 8.8	57.0 \pm 10.2	72.1 \pm 13.8
Western Redcedar (number stems > 50 cm/ha)	21.7 \pm 13.0	37.0 \pm 8.8	14.3 \pm 5.7
Amabilis Fir (number stems > 50 cm/ha)	1.1 \pm 0.7	14.0 \pm 5.6	5.0 \pm 2.2
Snags* (number stems > 50 cm/ha)	21.1 \pm 3.9	16.0 \pm 2.9	17.1 \pm 6.2
Distance to Patch of Old-Growth Forest < 50/ha (m)	630 \pm 145	610 \pm 85	1515 \pm 315
Old-Growth Forest within 2 km of the Patches (% of the area)	31.1 \pm 5.6	32.0 \pm 12.3	12.9 \pm 4.4
Number of Years Patches Were Isolated	21.3 \pm 3.2	17.0 \pm 2.8	16.7 \pm 3.2

*Standing dead trees > 5 m tall.

ated heterogeneous forests in those patches. Within the 500- and 2500-ha patches, we found the largest areas within the patches dominated by Douglas fir and western hemlock (420 ha) and by western hemlock, red cedar, and amabilis fir (1100 ha), respectively; we placed the stations at the centers of those areas.

We surveyed birds using point counts (Hutto et al. 1986; Koford et al. 1994) during the period that birds were establishing territories and attracting mates because breeding birds were most detectable at that time (Best 1981; Skirvin 1981). In our study areas, the period of intense territoriality extends throughout spring because some resident species breed during March and April (Campbell et al. 1990), whereas some of the migrating species do not arrive until May (Campbell et al. 1990). For logistical reasons we did not wish to conduct surveys between 1 March and 30 June. In addition, as much as was possible we wished to avoid counting migrating birds and family groups because those individuals move through areas where they do not breed (Best 1981). Consequently, during 1991 we surveyed birds within the Nimpkish-fir patches every 6 to 14 days between 12 April and 20 June (nine sampling periods). Based on those data we determined that 97% of the bird species at a station were detected after six surveys. Consequently, we conducted only six surveys within patches during 1992 (between 29 April and 11 June). To have comparable data between 1991 and 1992, we included only six of the surveys from 1991 with those surveys conducted between 28 April and 16 June.

Point counts were 10 minutes in duration, and all counts were conducted between first light and one hour past sunrise. During each point count the number of birds seen or heard within 100 m of the station were recorded for each species. Point counts were not conducted during rainy or windy mornings because birds were less detectable under those conditions (O'Connor & Hicks 1980; Robbins 1981). Birds that flew over but that did not land in trees or on the ground were not included in the analyses. Depending on the accessibility of the stations, either one or two patches were visited by an observer during a morning. Patches were surveyed an equal number of times by all observers.

We categorized species as old-growth species or non-old-growth species based on whether their abundance differed significantly among successional stages of coastal forests on Vancouver Island (Bryant et al. 1993; Seip & Savard, Ministry of Forests, Victoria, British Columbia; unpublished report 1990; Manning et al., Canadian Wildlife Service, Delta, British Columbia, unpublished report 1992). Categorization from those local studies was very similar to that suggested by the large-scale and more-intensives studies done in the U.S. in Washington and Oregon (Ruggiero et al. 1991). We also categorized old-growth species based on whether they used open cup-shaped nest or cavity nests (Godfrey

1986; Campbell et al. 1990; Semenchuk 1992) and non-old-growth species as potential predators or competitors of old-growth species (Godfrey 1986; Campbell et al. 1990; Semenchuk 1992).

Analyses of Richness by Patch Size

We recorded bird species as present at the patch center if they were detected during point counts at either station within the patch during any of the sampling periods. To evaluate relationships between bird species richness and patch size we used analyses of covariance (ANCOVA) with habitat type/geographic location (Nimpkish-fir, Nimpkish-hemlock, Shawnigan-hemlock) included as a categorical variable to reduce residual variation (SAS 1988). Patch size was logarithmically transformed in the analyses to remove heteroscedasticity from the data; other transformations and higher-order polynomial terms did not add significantly to the relationships. To avoid pseudoreplication (Hurlbert 1984), data that were collected from the Nimpkish-fir patches during 1992 (those patches were surveyed during both 1991 and 1992) were not included in the analyses.

The degree to which the landscape around a patch is fragmented also may affect species richness within the patch because inter-patch migration may be negatively related to patch isolation (Rosenberg & Raphael 1986; Martin & LePart 1989; Saunders 1990). Therefore, we computed two measures of landscape fragmentation: (1) distance to the nearest patch of old-growth forest that was greater than 50 ha and (2) amount of old-growth forest within 2 km of the patches. Both measures were determined from satellite images of the study areas. Another aspect of fragmentation that may influence species richness is length of time the remnant patch has been isolated because (1) the contrast between the remnant patch and the surrounding logged area may decrease as trees in the logged areas regenerate, and (2) as a consequence of low reproduction and recruitment some species may disappear from remnant patches over time. We used harvesting records to determine the number of years each patch had been isolated. None of the patches had all of the surrounding forest removed in a single year. Consequently, we calculated the mean number of years since the surrounding forest had been harvested, with age of harvest weighted by the length of edge of that age. We used multiple regression to evaluate the relative importance of each of the fragmentation variables. In those analyses, the influence of other fragmentation variables were "partialled out" before the influence of the variable in question was evaluated (SAS 1988). We report the partial F and partial R^2 statistics.

Analyses of Abundance by Patch Size

The choice of metric to be used as our index of abundance, and the analyses to be used on those metrics, was

not obvious because all metrics and analyses had weakness. Many species, although present at a patch center, were detected only rarely during the censuses in the patch, and consequently the mean or maximum number detected were more useful indices than the median number detected (median number detected often was zero). Mean and maximum number detected, however, were inflated by groups of migrants passing through remnant patches; some migrants, especially late migrants, were expected to have been present during May and June (Campbell et al. 1990). The probability of detecting a species (the fraction of the point counts in which a species was detected) was influenced less by migrating individuals, but no estimate of abundance was present in that measurement. For each species we chose to calculate three indices of presence/abundance (mean, maximum, and probability of occurrence) based on point counts ($n = 12$) at each of the patch centers and to compare results among the three sets of indices. We used ANCOVA (SAS 1988), with patch type included as a categorical variable, to evaluate the relationships between indices of presence/abundance and patch size. Patch size was logarithmically transformed in those analyses to remove heteroscedasticity. To avoid pseudoreplication (Hurlbert 1984) we did not include data that were collected from the Nimpkish-fir patches during 1992.

Assumptions of ANCOVA were not satisfied in the above analyses because the residuals were not normally distributed (Zar 1984); many species were absent from many of the patches, resulting in many zeros. We employed a fourth type of analysis, logistic regression, using all point counts within each of the patches. In those analyses, habitat type/geographic area and survey period were included as categorical variables, point-count station was included as a categorical variable nested within patches, and patch size was logarithmically transformed

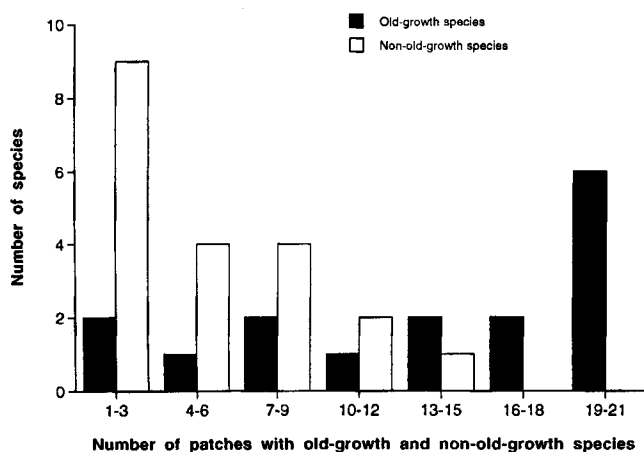


Figure 1. Frequency histogram of the number of patches of old-growth forest in which old-growth species and non-old-growth species were detected.

and included as a continuous variable (SAS 1988). We were unable to include survey period as a repeated measure because with our sparse data, those analyses became singular and the tests were undefined. Therefore, we have not accounted for the autocorrelation of the repeated censuses in this set of analyses (censuses were conducted at each station six times), and the tests will be overly liberal (Scott & Holt 1982). The shape (slope) of the relationships, however, will be correct (Scott & Holt 1982). We compared results from this set of analyses with those from the three sets of more-conservative analyses that were conducted previously. For each species, the average slope for the relationship was considered negative if three or four of the analyses had negative slopes, positive if three or four of the analyses had positive slopes, and zero if two of the analyses had negative slopes and two had positive slopes.

Results

Richness and Patch Size

Thirty-six bird species (16 old-growth species and 20 non-old-growth species) were detected in at least one of the remnant patches of old-growth forest (Appendix). Most old-growth species were detected in many patches, whereas most of the non-old-growth species were detected in only a few patches (Fig. 1).

The number of non-old-growth bird species found at the patch center was negatively related to patch size (Fig. 2b; $F = 13.7$, $p < 0.01$, $df = 1, 17$, $R^2 = 0.27$) but not related to distance to the nearest patch of old-growth forest greater than 50 ha ($F = 0.1$, $p = 0.79$, $df = 1, 17$, $R^2 < 0.01$), amount of old-growth forest within 2 km of the patch ($F = 0.3$, $p = 0.60$, $df = 1, 17$, $R^2 < 0.01$), or number of years since the patch had been isolated ($F = 0.5$, $p = 0.48$, $df = 1, 17$, $R^2 = 0.10$). The number of non-old-growth species classified as potential predators was not related to patch size (Fig. 3a; $F = 0.4$, $p = 0.55$, $df = 1, 17$, $R^2 = 0.02$). Number of non-old-growth species classified as potential competitors, however, was negatively related to patch size (Fig. 3b; $F = 14.2$, $p < 0.01$, $df = 1, 17$, $R^2 = 0.27$). Although Brown-headed Cowbirds, a brood parasite, were detected in urban areas approximately 15 km from the patches that we surveyed, none was observed either during the censuses or incidentally in or near the patches during our study.

The number of old-growth species found at the patch center was not related to patch size (Fig. 2a; $F = 1.1$, $p = 0.30$, $df = 1, 17$, $R^2 = 0.05$). When measures of landscape fragmentation were included as covariates in the analyses, the richness of old-growth birds at the patch center was negatively related to patch size and not positively related, as was predicted ($F = 5.6$, $p = 0.03$, $df =$

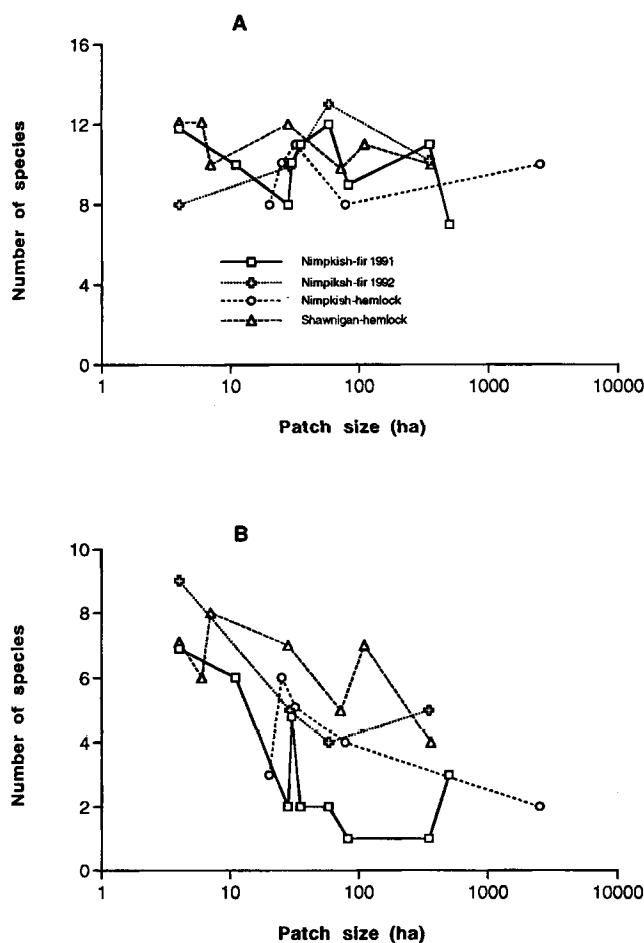


Figure 2. Relationship between bird species richness at the patch center and patch size within remnant patches of old-growth forests on Vancouver Island, Canada: old-growth (a) and non-old-growth species (b).

1, 14, $R^2 = 0.20$). The number of old-growth species was not related to measures of fragmentation (distance to the nearest patch of old-growth forest greater than 50 ha: $F < 0.1$, $p = 0.91$, $df = 1$, 17, $R^2 < 0.01$; amount of old-growth forest within 2 km of the patch: $F < 0.1$, $p = 0.95$, $df = 1$, 17, $R^2 < 0.01$; number of years since the patch had been isolated: $F = 2.0$, $p = 0.12$, $df = 1$, 17, $R^2 = 0.09$). The number of old-growth species that nested in open, cup-shaped nests and cavities did not vary in relation to patch size (Fig. 4; cup nesters: $F = 1.9$, $p = 0.19$, $df = 1$, 17, $R^2 = 0.10$; cavity nesters: $F = 0.8$, $p = 0.39$, $df = 1$, 17, $R^2 = 0.03$).

Abundance and Patch Size

In analysis involving the first three measures of presence/abundance were used only between 2 and 4 of the 20 non-old-growth species had statistically significant relationships between indices of presence/abundance and

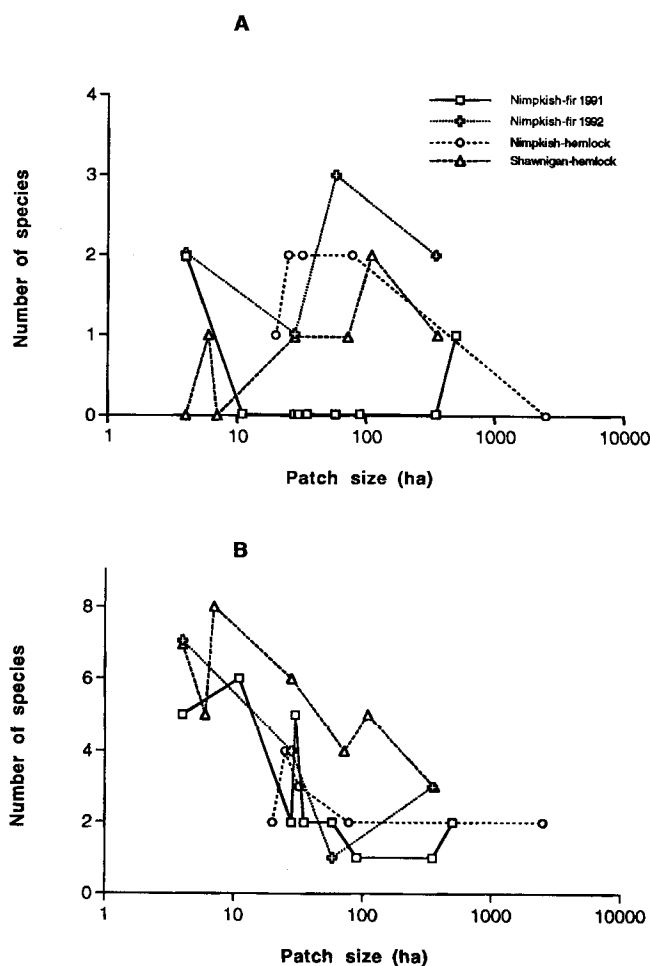


Figure 3. Relationships between richness of non-old-growth bird species at the patch center and patch size within remnant patches of old-growth forests on Vancouver Island, Canada: potential predators (a) and potential competitors (b).

patch size (Table 2). Slightly more non-old-growth species ($n = 5$) had statistically significant relationships with patch size in the logistic regression analyses (Table 2), but, as discussed, those tests were liberal. More non-old-growth species had negative ($n = 17$) than positive ($n = 3$) average slopes (Table 2), and that was statistically different from a 1:1 ratio that would have been expected at random ($\chi^2 = 9.8$, $p < 0.01$, $df = 1$). All non-old-growth species that were potential egg and nestling predators had negative average slopes for the relationships between presence/abundance and patch size, although none of these relationships, even using the liberal logistic regression analyses, were statistically significant (Table 2). Thirteen of the 16 non-old-growth species that were potential competitors had negative average slopes (Table 2), and that was statistically different from a 1:1 ratio that would have been expected at random ($\chi^2 = 7.1$, $p < 0.01$, $df = 1$).

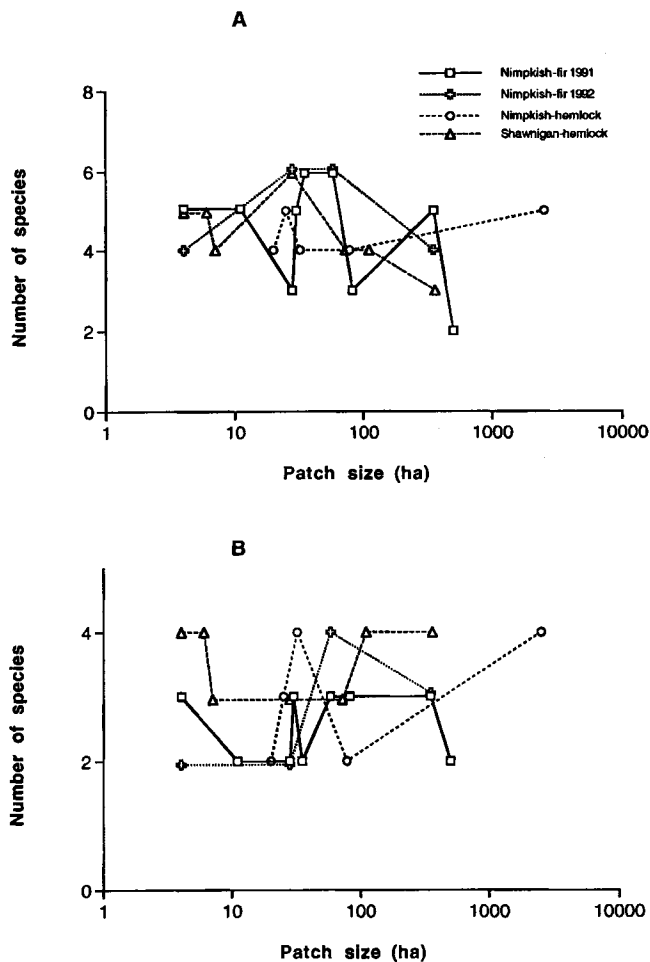


Figure 4. Relationships between richness of old-growth bird species at the patch center and patch size within remnant patches of old-growth forests on Vancouver Island, Canada: cup-nesting (a) and cavity-nesting birds (b).

In analyses involving the first three measures of presence/abundance were used, few (between one and three) of the old-growth species had statistically significant relationships between indices of presence/abundance and patch size (Table 2). More old-growth species had statistically significant relationships with patch size when the logistic regression analyses were used (Table 2), but those tests were liberal. Slightly more old-growth species had negative ($n = 8$) rather than positive ($n = 6$) average slopes (Table 2), but that trend was not statistically different from a 1:1 ratio that would have been expected at random ($\chi^2 = 0.3$, $p = 0.60$, $df = 1$). Although there were too few species to test whether old-growth species nesting in open cup-shaped nests differed from those nesting in cavities, the patterns were identical for the two groups (species with open cup-shaped nests: four positive and four negative average slopes; species nesting in cavities: two positive and two negative average slopes; Table 2).

Discussion

We hypothesized that old-growth bird species, especially those having open cup-shaped nests, would be affected negatively at the center of small remnant patches of old-growth forest because species living on the edge and outside the patches would (1) depredate eggs and young (Askins et al. 1990; Andren 1992); (2) increase the amount of competition (Saunders et al. 1991); and (3) possibly parasitize their nests (Gates & Gysel 1978). We sampled a range of patch sizes to obtain some patches small enough that many non-old-growth species would be present at the center and other patches large enough that few non-old-growth species would be present at the center. Those conditions appear to have been achieved, because richness of non-old-growth species at the patch center was negatively related to patch size. In addition, although most of the relationships between the abundance of non-old-growth species at the patch center and patch size were not statistically significant, many more species had negative trends than would have been expected at random. Thus, the influence of non-old-growth species also should have been negatively related to patch size. Our results from old-growth species, however, do not support the hypothesis that old-growth species would be affected detrimentally at the center of small remnant patches of old-growth forest; neither richness nor abundance of old-growth birds was related to patch size.

Because we found only weak support for our predictions, it is important to evaluate the power of the tests (Peterman 1990; Shrader-Frechette & McCoy 1992). The tests were powerful enough to detect relationships 80% of the time if 39% of the variation in species richness and abundance was explained by variation in patch size, and they were able to detect relationships 50% of the time if 19% of the variation in species richness and abundance was explained by variation in patch size (calculations follow Cohen 1988). Consequently, we are confident that the richness and abundance of old-growth birds were not strongly related to patch size. Due to our small sample size ($n = 21$), our tests may have lacked the power to detect weak relationships between richness/abundance and patch size (Cohen 1988).

Two other studies evaluating the relationship between the richness and abundance of birds and patch size have been conducted within coastal montane forests of western North America (Rosenberg & Raphael 1986; Lehmkuhl et al. 1991). Those studies also provide only weak support for the fragmentation paradigm that appears to be common for other areas; few old-growth species were affected negatively in small, remnant patches of old-growth forest. Nest parasitism by Brown-headed Cowbirds, although implicated as having negative effects within forest fragments in studies from eastern North America (Gates & Gysel 1978; Wilcove 1985), was

Table 2. Relationships between the presence/abundance of birds and patch size within remnant patches of old-growth forests on Vancouver Island, Canada.^a

Species	Species Type ^b	Mean Number ^c			Maximum Number ^c			Probability of Occurrence ^c			Logistic Regression ^d			Average Slope
		F	p	Slope	F	p	Slope	F	p	Slope	χ ²	p	Slope	
Old-growth Species														
Sharp-shinned Hawk	O	1.7	0.21	-	0.3	0.57	-	0.9	0.35	-	0.7	0.40	+	-
Marbled Murrelet	O	0.2	0.65	+	0.1	0.80	+	1.2	0.79	+	0.2	0.67	+	+
Hammond's Flycatcher	O	2.4	0.14	-	3.6	0.07	-	3.9	0.07	-	9.4*	<0.01*	-	-
Pacific-slope Flycatcher	O	5.4*	0.03*	-	2.4	0.14	-	1.8	0.20	-	5.5*	0.02*	-	-
Varied Thrush	O	0.6	0.45	+	0.3	0.58	+	2.0	0.18	+	7.3*	0.01*	+	+
Townsend's Warbler	O	0.6	0.46	-	1.9	0.18	-	0.3	0.60	-	0.1	0.72	+	-
Red Crossbill	O	2.5	0.13	+	<0.1	0.97	+	1.6	0.22	+	4.7*	0.03*	+	+
Pine Siskin	O	5.4*	0.03*	+	1.5	0.24	+	5.0*	0.04*	+	4.2*	0.04*	+	+
Red-breasted Sapsucker	H	1.1	0.31	+	3.8	0.07	+	<0.1	0.85	-	<0.1	0.90	-	0
Hairy Woodpecker	H	3.2	0.09	-	<0.1	0.92	-	3.1	0.10	-	5.1*	0.02*	-	-
Pileated Woodpecker	H	0.1	0.80	-	<0.1	0.91	+	0.1	0.77	-	<0.1	0.86	-	-
Chestnut-backed Chickadee	H	1.3	0.27	+	4.6*	0.05*	+	1.4	0.26	+	3.6*	0.05*	+	+
Red-breasted Nuthatch	H	6.4*	0.02*	+	3.4	0.08	+	6.2*	0.02*	+	9.4*	<0.01*	+	+
Brown Creeper	E	0.1	0.81	+	<0.1	0.89	-	0.6	0.44	-	<0.1	0.99	+	0
Winter Wren	E	1.4	0.26	-	2.4	0.14	-	0.3	0.58	-	2.4	0.12	-	-
Golden-crowned Kinglet	E ^c	1.1	0.30	-	<0.1	0.99	+	1.0	0.33	-	2.5	0.12	-	-
Non-old-growth Species														
Gray Jay	P	0.2	0.68	-	<0.1	0.89	+	0.1	0.79	-	0.1	0.74	-	-
Steller's Jay	P	1.5	0.24	-	1.3	0.28	-	1.6	0.24	-	0.8	0.38	-	-
Northwestern Crow	P	<0.1	0.97	-	<0.1	0.97	-	<0.1	0.97	-	2.2	0.13	-	-
Common Raven	P	0.5	0.50	-	0.5	0.50	-	0.5	0.50	-	0.2	0.64	-	-
Ruffed Grouse	C	2.6	0.13	-	2.6	0.13	-	2.6	0.13	-	1.1	0.29	-	-
Band-tailed Pigeon	C	10.5*	<0.01*	+	19.1*	<0.001*	+	10.5*	<0.01*	+	8.7*	<0.01*	+	+
Rufous Hummingbird	C	2.7	0.12	-	3.7	0.07	-	2.7	0.12	-	2.2	0.14	-	-
Northern Flicker	C	0.3	0.60	+	0.1	0.76	+	0.1	0.74	+	0.3	0.61	-	+
Olive-sided Flycatcher	C	1.8	0.20	-	3.0	0.10	-	2.0	0.18	-	9.1*	<0.01*	-	-
Swainson's Thrush	C	3.7	0.07	-	3.2	0.09	-	5.3*	0.03*	-	6.0*	0.01*	-	-
Hermit Thrush	C	0.6	0.46	-	6.7*	0.02*	-	0.1	0.81	-	0.1	0.75	-	-
American Robin	C	4.6*	0.05*	-	4.8*	0.04*	-	4.3	0.06	-	12.8*	<0.001*	-	-
Red-eyed Vireo	C	0.5	0.50	-	0.5	0.50	-	0.5	0.50	-	0.4	0.50	-	-
Black-throated Gray Warbler	C	1.2	0.29	-	1.2	0.30	-	1.0	0.34	-	0.5	0.49	-	-
MacGillivray's Warbler	C	1.5	0.24	-	2.4	0.14	-	1.6	0.22	-	4.9*	0.03*	-	-
Common Yellowthroat	C	1.4	0.26	-	1.2	0.29	-	1.4	0.26	-	2.9	0.08	-	-
Wilson's Warbler	C	3.3	0.09	-	3.3	0.09	-	3.3	0.09	-	2.3	0.13	-	-
Rufous-sided Towhee	C	0.8	0.39	-	0.8	0.39	-	0.8	0.39	-	0.3	0.59	-	-
Song Sparrow	C	1.6	0.23	-	2.2	0.15	-	1.8	0.19	-	2.5	0.12	-	-
Dark-eyed Junco	C	0.5	0.50	+	6.2*	0.02*	+	2.5	0.13	+	0.2	0.64	+	+

^a Tests were conducted using four different metrics and analyses. Slopes were presented as positive or negative; and average slope was considered negative if three or four of the analyses had negative slopes, positive if three or four of the analyses had positive slopes, and zero if two of the analyses had negative and two of the analyses had positive slopes. Statistically significant relationships are marked with an asterisk (*).

^b Old-growth species were categorized as nesting in open cup-shaped nests (O), cavities (H), or enclosed nests (E). Non-old-growth species were categorized as potential predators (P) or potential competitors (C).

^c df = 2.

^d df = 1.

^e Nest is a deep cut and thus is similar to an enclosed nest.

not detected within or adjacent to the patches that we surveyed. In addition, this species was not detected, or was detected only rarely, in other studies conducted in forested landscapes of coastal western North America (Manuwal & Huff 1987; Carey et al. 1991; Gilbert & Allwine 1991; Huff & Raley 1991; Manuwal 1991; Ralph et al. 1991; Ruggiero et al. 1991; Bryant et al. 1993; Seip & Savard, Ministry of Forests, Victoria, British Columbia, unpublished report 1990). Consequently, Brown-headed

Cowbirds probably have few negative effects on birds living within the forested landscapes that we studied.

Gray Jays (*Perisoreus canadensis*), Steller's Jays (*Cyanocitta stelleri*), Northwestern Crows (*Corvus caurinus*), and Common Ravens (*Corvus corax*) were the most common avian predators in coastal montane forests and those species may prey upon eggs and young in open cup-shaped nests (Andren 1992). The richness of corvid species at the patch center, however, was not re-

lated to patch size. In addition, although all corvid species tended to be more abundant at the center of small rather than large patches, those trends were not statistically significant. In other studies within coastal montane old-growth forests, the abundance of corvids also was not significantly related to patch size (Rosenberg & Raphael 1986; Lehmkuhl et al. 1991). In the landscapes we studied, corvids may have similar effects in both small and large remnant patches of old-growth forest. We stress that our study and studies by Rosenberg and Raphael (1986) and Lehmkuhl et al. (1991) should be interpreted as preliminary tests of the hypotheses only, because the viability of populations within the remnant patches were not evaluated (Van Horne 1983; Kellner et al. 1992).

Contrary to the results from coastal montane forests of western North America, strong relationships between the richness/abundance of forest birds and patch size occur in other parts of the world (Freemark & Merriam 1986; Askins et al. 1987; Askins et al. 1990; Daniels et al. 1990; Saunders 1990; Opdam 1991). There are three plausible explanations for the relatively weak relationships that we found. First, population viability may have been strongly related to patch size even though abundance of individuals was not (Van Horne 1983). There were extensive areas of old-growth forest within 10 km of the patches that we surveyed, and populations within our small patches may have been maintained by immigration from those other areas (Saunders et al. 1991). The viability of populations within remnant patches can be evaluated only if reproduction, recruitment, and inter-patch migration are measured in each of the patches (Kellner et al. 1992; Vickery et al. 1992).

Second, forest fragmentation may be less detrimental in some landscapes than in others (Hansen & Urban 1992). In the coastal montane landscape that we studied, physiography and natural phenomena (such as topographical relief, fires, wind, disease, and stream channels) maintained abundant heterogeneity in the forests prior to the area being partially logged (Hansen et al. 1991; Meidinger & Pojar 1991). Because of this natural heterogeneity, wildlife species would have evolved in contact with species from many forest types and may have been able to interact effectively with species from those other forest types (Hansson & Angelstram 1991; Hansen & Urban 1992). In support of that hypothesis, most birds that live in montane old-growth forests of western North America are present in all ages of forest, although at least some of the species are at lower densities in the young rather than in the old-growth forests (Rosenberg & Raphael 1986; Manuwal & Huff 1987; Ruggiero et al. 1991). It would be beneficial to know whether the populations of old-growth species that were present in the younger forests were viable or whether they were maintained by immigration (Lehmkuhl et al. 1991).

Third, negative effects on old-growth birds in small patches of old-growth forest may have been low because the contrast between logged areas and the residual patches was relatively low. Most previous studies of forest fragmentation have been conducted in areas where fragmentation was caused by agricultural development (Freemark & Merriam 1986; Saunders 1990) or urbanization (Recher & Serventy 1991), and the inter-patch habitats differed greatly from the remnant forest patches. Within forested landscapes, however, logged areas redevelop some of the characteristics of natural forests (Spies & Franklin 1991), and the contrast between forest patches and the inter-patch matrix may be lower than that found within agricultural areas (Hanson et al. 1991). Thus, different types of species may have been present in agricultural and urban landscapes (Brown-headed Cowbird, for example) than within logged landscapes, and the effects on old-growth species may have been relatively small within logged landscapes (Hansson & Angelstram 1991; Rudnický & Hunter 1993). To evaluate the generality of these three potential hypotheses, it will be necessary to study a wide range of habitats and human disturbances.

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Literature Cited

- Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 7:794-804.
- Askins, A. R., M. J. Philbrick, and D. S. Sugeno. 1987. Relationships between regional abundance of forest and the composition of forest bird communities. *Biological Conservation* 39:129-152.
- Askins, A. R., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Pages 1-57 in D. M. Powers, editor. *Current ornithology*, vol. 7. Plenum Press, New York.
- Best, L. B. 1981. Seasonal changes in detection of individual bird species. *Studies in Avian Biology* 6:252-261.
- Bryant, A. A., J.-P. Savard, and R. T. McLaughlin. 1993. Avian communities in old-growth and managed forests of western Vancouver Island, British Columbia. Technical report series no 167. Canadian Wildlife Service, Delta, British Columbia, Canada.
- Bull, E. L., and R. S. Holthausen. 1993. Habitat use and management of Pileated Woodpeckers in northwestern Oregon. *Journal of Wildlife Management* 57:335-345.

- Burdick, D. M., D. Cushman, R. Hamilton, and J. G. GosseLink. 1989. Faunal changes and bottemland hardwood forests loss in the Tenas watershed, Louisiana. *Conservation Biology* 3:282-292.
- Campbell, R. W., N. E. Dawe, I. Mct. Cowan, J. M. Cooper, G. W. Kaiser, and M. C. McNall. 1990. The birds of British Columbia, vol. 2. The Royal British Columbia Museum, Victoria, British Columbia, Canada.
- Carey, A. B., M. M. Hardt, S. P. Horton, and B. L. Biswell. 1991. Spring bird communities in the Oregon coast Range. Pages 123-144 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*. Lawrence Erlbaum, Hillsdale, New Jersey.
- da Fonseca, G. A., and J. G. Robinson. 1990. Forest size and structure: competitive and predatory effects on small mammal communities. *Biological Conservation* 53:265-294.
- Daniels, R. J., N. V. Joshi, and M. Gadgil. 1990. Changes in the bird fauna of Uttara Kannada, India, in relation to changes in land use over the past century. *Biological Conservation* 52:37-48.
- Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity on bird assemblages in temperate forest fragments. *Biological Conservation* 36:115-141.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging outcome in field-forest edges. *Ecology* 59:871-883.
- Gilbert, F. F., and R. Allwine. 1991. Spring bird communities in the Oregon Cascade range. Pages 145-160 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- Godfrey, W. E. 1986. *The birds of Canada*. National Museum of Natural Sciences, Ottawa, Ontario.
- Hansen, A. J., and D. L. Urban. 1992. Avian response to landscape pattern: the role of species' life histories. *Landscape Ecology* 7:163-180.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. *BioScience* 41:382-392.
- Hansson, L., and P. Angelstram. 1991. Landscape-ecology as a theoretical basis for nature conservation. *Landscape Ecology* 5:191-201.
- Huff, M. H., and C. M. Raley. 1991. Regional patterns of diurnal breeding bird communities in Oregon and Washington. Pages 177-206 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.
- Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. *The Auk* 103:593-602.
- Kellner, C. J., J. D. Brawn, and J. R. Karr. 1992. What is habitat suitability and how should it be measured? Pages 476-488 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001*. Elsevier Science Publishers, London.
- Koford, R. R., J. B. Dunning, C. A. Ribic, and D. M. Finch. 1994. A glossary for avian conservation biology. *Wilson Bulletin* 106:121-137.
- Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55:77-92.
- Lehmkuhl, J. F., L. E. Ruggiero, and P. A. Hall. 1991. Landscape patterns of forest fragmentation and wildlife richness and abundance in the southern Washington Cascade range. Pages 425-442 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- Lovejoy, T. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 in M. E. Soulié, editor. *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Manuwal, D. A. 1991. Spring bird communities in the southern Washington Cascade range. Pages 161-176 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- Manuwal, D. A., and M. H. Huff. 1987. Spring and winter bird populations in a Douglas-fir forest sere. *Journal of Wildlife Management* 51:586-595.
- Martin, J.-L., and J. LePart. 1989. Impoverishment in the bird community of a Finnish archipelago: the role of island size, isolation and vegetation structure. *Journal of Biogeography* 16:159-172.
- Meidinger, D., and J. Pojar. 1991. *Ecosystems of British Columbia*. Report series no. 6. British Columbia Ministry Of Forests, Victoria, British Columbia, Canada.
- O'Connor, R. J., and R. J. Hicks. 1980. The influence of weather conditions on the detections of birds during common bird census fieldwork. *Bird Study* 27:137-151.
- Opdam, P. 1991. Metapopulation theory and habitat fragmentation: A review of holarctic breeding bird studies. *Landscape Ecology* 5:93-106.
- Pahl, L. I., J. W. Winter, and G. Heinsohn. 1988. Variation in responses of arboreal marsupials to fragmentation of tropical rainforest in northeastern Australia. *Biological Conservation* 46:71-82.
- Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8:17-26.
- Peterman, R. M. 1990. Statistical power analysis can improve fisheries research and management. *Canadian Journal of Fisheries and Aquatic Science* 47:2-15.
- Ralph, C. J., P. W. Paton, and C. A. Taylor. 1991. Habitat association patterns of breeding birds and small mammals in Douglas-fir/hardwood stands in northern California and southwestern Oregon. Pages 425-442 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- Recher, H. F., and D. L. Serventy. 1991. Long term changes in the relative abundance of birds in Kings Park, Perth, Western Australia. *Conservation Biology* 5:90-102.
- Robbins, C. S. 1981. Bird activity levels related to weather. *Studies in Avian Biology* 6:301-310.
- 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.
- Rudnicki, T. C., and M. L. Hunter. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57:358-364.
- Ruggiero, L. F., L. L. Jones, and K. B. Aubry. 1991. Plant and animal habitat associations in Douglas-fir forests of the pacific northwest: an overview. Pages 447-462 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- SAS. 1988. *SAS/STAT users guide*. Release 6.03. SAS Institute, Cary, North Carolina.
- Saunders, D. A. 1989. Changes in the avifauna of a region, district and remnant as a result of fragmentation of native vegetation: the wheatbelt of Western Australia: a case study. *Biological Conservation* 50:99-135.
- Saunders, D. A. 1990. Problems of survival in an extensively cultivated landscape: the case of Carnsby's cockatoo *Calyptorhynchus fuliginerosus latirostris*. *Biological Conservation* 54:277-290.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- Scott, A. J., and D. Holt. 1982. The effect of two stage sampling on ordinary least squares methods. *Journal of the American Statistical Association* 77:848-854.
- Semenchuk, G. P. 1992. *The atlas of breeding birds of Alberta*. Federation of Alberta Naturalists, Edmonton, Alberta, Canada.
- Shrader-Frechette, K. S., and E. D. McCoy. 1992. Statistics, costs and rationality in ecological inference. *TREE* 7:96-99.
- Skirvin, A. A. 1981. Effect of time of day and time of season on the number of observations and density estimates of breeding birds. *Studies in Avian Biology* 6:271-274.

- Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests. Pages 91-110 in *Wildlife and vegetation of unmanaged Douglas-fir forests*. PNW-GTR-285. U.S. Forest Service, Portland, Oregon.
- Usher, M. B. 1988. Biological invasions of nature reserves: a search for generalisations. *Biological Conservation* 44:119-135.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- Vickery, P. D., M. L. Hunter, and J. V. Welks. 1992. Is density an indicator of breeding success? *The Auk* 109:706-710.
- Villard, M.-A., P. R. Martin, and C. G. Drummond. 1991. Habitat fragmentation and pairing success in the Ovenbird (*Seturus aurocapillus*). *The Auk* 110:759-768.
- Wenny, D. G., R. L. Clawson, J. Foabory, and S. L. Sheriff. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. *Condor* 95:968-979.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:121-124.
- Yahner, R. H., and C. A. DeLong. 1992. Avian predation and parasitism on artificial nests and eggs in two fragmented landscapes. *Wilson Bulletin* 104:162-168.
- Zar, J. H. 1984. *Biostatistical analyses*. 2nd edition. Prentice Hall, Englewood Cliffs, New Jersey.

Appendix

Percentage of point counts in which species were detected within remnant patches* of old-growth forests on Vancouver Island, Canada.

Common Name	Scientific Name	Patch Size (ha) Nimpkish-fir 1991								
		4	11	28	30	35	58	82	350	500
Old-growth Species										
Sharp-shinned Hawk	<i>Accipiter straitus</i>	0	0	0	0	0	0	0	0	0
Marbled Murrelet	<i>Brachyramphus marmoratus</i>	0	0	0	0	0	8.3	0	0	0
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	<i>Picoides villosus</i>	58.3	8.3	0	16.7	8.3	0	0	16.7	0
Pileated Woodpecker	<i>Dryocopus pileatus</i>	0	0	0	0	0	8.3	33.3	0	0
Hammond's Flycatcher	<i>Empidonax hammondi</i>	50.0	50.0	25.0	50.0	66.7	25.0	16.7	58.3	0
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	25.0	50.0	0	41.7	8.3	8.3	50.0	8.3	0
Chestnut-backed Chickadee	<i>Parus rufescens</i>	25.0	75.0	50.0	50.0	75.0	33.3	83.3	66.7	41.7
Red-breasted Nuthatch	<i>Sitta canadensis</i>	8.3	0	25.0	8.3	0	25.0	25.0	25.0	8.3
Brown Creeper	<i>Certhia americana</i>	50.0	33.3	66.7	50.0	50.0	33.3	25.0	50.0	50.0
Winter Wren	<i>Troglodytes troglodytes</i>	75.0	66.7	91.7	91.7	83.3	91.7	100.0	66.7	91.7
Golden-crowned Kinglet	<i>Regulus satrapa</i>	50.0	50.0	83.3	0	75.0	33.3	58.3	33.3	75.0
Varied Thrush	<i>Ixoreus naevius</i>	16.7	66.7	41.7	50.0	41.7	25.0	50.0	33.3	58.3
Townsend's Warbler	<i>Dendroica townsendi</i>	25.0	25.0	50.0	8.3	41.7	33.3	0	41.7	0
Red Crossbill	<i>Loxia curvirostra</i>	8.3	8.3	0	16.7	25.0	0	0	16.7	0
Pine Siskin	<i>Carduelis pinus</i>	0	0	0	0	8.3	8.3	0	0	33.3
Non-old-growth Species										
Ruffed Grouse	<i>Bonasa umbellus</i>	8.3	0	0	0	0	0	0	0	0
Band-tailed Pigeon	<i>Columba fasciata</i>	0	0	0	0	0	0	0	0	0
Rufous Hummingbird	<i>Selasphorus rufus</i>	8.3	0	0	0	0	0	0	0	0
Northern Flicker	<i>Colaptes auratus</i>	0	8.3	0	8.3	0	8.3	16.7	0	8.3
Olive-sided Flycatcher	<i>Contopus borealis</i>	0	33.3	0	0	0	0	0	0	0
Gray Jay	<i>Perisoreus canadensis</i>	0	0	0	0	0	0	0	0	0
Steller's Jay	<i>Cyanocitta stelleri</i>	8.3	0	0	0	0	0	0	0	0
Northwestern Crow	<i>Corvus caurinus</i>	8.3	0	0	0	0	0	0	0	8.3
Common Raven	<i>Corvus corax</i>	0	0	0	0	0	0	0	0	0
Swainson's Thrush	<i>Catbarus ustulatus</i>	8.3	0	0	0	0	0	0	0	0
Hermit Thrush	<i>Catbarus guttatus</i>	0	0	0	0	0	0	0	0	0
American Robin	<i>Turdus migratorius</i>	66.7	16.7	8.3	25.0	25.0	8.3	0	33.3	8.3
Red-eyed Vireo	<i>Vireo olivaceus</i>	0	0	0	0	0	0	0	0	0
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	0	16.7	25.0	8.3	8.3	0	0	0	0
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	8.3	0	0	16.7	0	0	0	0	0
Common Yellowthroat	<i>Geothlypis trichas</i>	0	8.3	0	0	0	0	0	0	0
Wilson's Warbler	<i>Wilsonia pusilla</i>	0	0	0	0	0	0	0	0	0
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>	0	8.3	0	8.3	0	0	0	0	0
Song Sparrow	<i>Melospiza melodia</i>	0	0	0	0	0	0	0	0	0
Dark-eyed Junco	<i>Junco hyemalis</i>	0	0	0	0	0	0	0	0	0

Appendix Continued

Common Name	Patch Size (ba) <i>Nimpkish-fir 1992</i>				Patch Size (ba) <i>Nimpkish-hemlock</i>					Patch Size (ba) <i>Sbawnigan-hemlock</i>						
	4	28	58	350	20	28	32	78	2500	4	6	7	28	72	110	360
Old-growth Species																
Sharp-shinned Hawk	0	0	33.3	0	0	0	0	0	0	8.3	0	0	8.3	0	0	0
Marbled Murrelet	0	0	0	0	0	0	0	0	0	8.3	0	0	0	0	16.7	0
Red-breasted Sapsucker	0	0	0	0	16.7	8.3	0	8.3	8.3	0	0	0	0	0	0	0
Hairy Woodpecker	16.7	0	16.7	41.7	0	0	25.0	0	8.3	33.3	8.3	33.3	8.3	16.7	25.0	8.3
Pileated Woodpecker	0	0	8.3	0	0	0	16.7	0	0	16.7	25.0	0	0	0	16.7	8.3
Hammond's Flycatcher	66.7	41.7	16.7	66.7	8.3	0	0	8.3	0	75.0	8.3	0	25.0	0	0	0
Pacific-slope Flycatcher	41.7	33.3	33.3	16.7	66.7	58.3	83.3	16.7	66.7	75.0	100.0	100.0	91.7	91.7	91.7	58.3
Chestnut-backed Chickadee	41.7	8.3	8.3	91.7	83.3	41.7	75.0	50.0	83.3	16.7	25.0	33.3	25.0	41.7	41.7	25.0
Red-breasted Nuthatch	0	41.7	8.3	8.3	0	8.3	8.3	0	16.7	8.3	16.7	41.7	33.3	33.3	16.7	75.0
Brown Creeper	0	0	25.0	25.0	16.7	8.3	25.0	0	0	33.3	25.0	16.7	25.0	25.0	8.3	33.3
Winter Wren	83.3	91.7	100.0	83.3	83.3	100.0	66.7	91.7	33.3	100.0	91.7	33.3	100.0	91.7	100.0	83.3
Golden-crowned Kinglet	91.7	75.0	83.3	8.3	66.7	66.7	66.7	50.0	41.7	66.7	83.3	83.3	83.3	91.7	66.7	41.7
Varied Thrush	41.7	58.3	66.7	91.7	58.3	83.3	33.3	33.3	58.3	50.0	75.0	16.7	66.7	83.3	91.7	75.0
Townsend's Warbler	8.3	41.7	8.3	0	0	0	0	0	0	0	0	0	0	0	0	0
Red Crossbill	0	41.7	25.0	8.3	16.7	41.7	41.7	16.7	75.0	0	41.7	8.3	8.3	58.3	16.7	8.3
Pine Siskin	0	16.7	0	0	0	8.3	8.3	0	33.3	0	8.3	16.7	8.3	16.7	0	0
Non-old-growth Species																
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Band-tailed Pigeon	0	0	0	0	0	0	0	0	8.3	0	0	0	0	8.3	25.0	33.3
Rufous Hummingbird	16.7	0	0	0	0	0	0	0	0	0	16.7	0	0	0	0	0
Northern Flicker	0	0	0	0	8.3	25.0	16.7	0	0	25.0	16.7	16.7	16.7	83.3	8.3	33.3
Olive-sided Flycatcher	0	16.7	0	25.0	0	16.7	0	0	0	8.3	0	8.3	8.3	8.3	0	0
Gray Jay	0	8.3	8.3	8.3	16.7	0	25.0	33.3	0	0	0	0	0	0	8.3	8.3
Steller's Jay	8.3	0	8.3	0	0	16.7	8.3	8.3	0	0	8.3	0	8.3	8.3	8.3	0
Northwestern Crow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Common Raven	8.3	0	8.3	8.3	0	8.3	0	0	0	0	0	0	0	0	0	0
Swainson's Thrush	16.7	16.7	0	0	0	0	0	8.3	0	16.7	8.3	8.3	0	0	8.3	0
Hermit Thrush	8.3	0	0	0	41.7	8.3	16.7	25.0	0	25.0	58.3	16.7	16.7	16.7	41.7	58.3
American Robin	58.3	8.3	50.0	0	0	0	8.3	0	0	25.0	0	58.3	33.3	0	0	0
Red-eyed Vireo	0	0	0	8.3	0	16.7	0	0	0	0	0	0	0	0	0	0
Black-throated Gray Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MacGillivray's Warbler	25.0	0	0	0	0	0	0	0	0	0	0	33.3	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0	0	0	0	0	0	16.7	8.3	0	0	0
Wilson's Warbler	0	0	0	0	0	0	0	0	0	8.3	8.3	0	0	0	0	0
Rufous-sided Towhee	8.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Song Sparrow	0	0	0	0	0	0	0	0	0	8.3	0	25.0	8.3	0	0	0
Dark-eyed Junco	8.3	8.3	0	25.0	0	0	0	0	8.3	0	0	0	0	0	25.0	0

* Patches were categorized by habitat type/geographic area and ordered based on size.

