LANDSCAPE MODIFICATION AND PATCH SELECTION: THE DEMOGRAPHY OF TWO SECONDARY CAVITY NESTERS COLONIZING CLEARCUTS

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ABSTRACT.—Current forestry practices radically modify habitat, particularly by increasing the frequency of early seral stages. We examined the demography of two secondary cavity nesters, the Mountain Bluebird (*Sialia currucoides*) and the Tree Swallow (*Tachycineta bicolor*), with respect to landscape changes. The study area contained a mosaic of clearcuts ranging from 3 to 27 years in age. The initial distribution of both species was uneven with respect to patch age. Experimental addition of nest boxes: (1) increased the number of nesting pairs of both species, and (2) expanded the age range of occupied patches. Nest-site availability was the primary limiting factor in young patches, but vegetation structure was increasingly important in determining occupation in older patches. Mountain Bluebird patch occupation and Tree Swallow density were best predicted by the proportion of trees 1 to 3 m in height. Although some patches contained multiple pairs of Mountain Bluebirds in natural cavities, experimental patches typically contained no more than one pair, even though excess nest boxes were available. The presence of nonbreeding floaters was an indication of nest-site limitation and suggested that Mountain Bluebirds sometimes defer breeding attempts rather than nest close to conspecifics. At low densities, Tree Swallows also were over-dispersed, but pairs saturated available nest boxes as density increased. Clutch size and number of chicks fledged from successful nests did not vary with patch age for either species, although swallows initiated clutches later in younger compared with older patches. Nest predation varied consistently with patch age; mean nest predation for both species was 86% ($n = 30$ pairs) in the youngest patches, 37% ($n = 34$) in mid-age patches, and 25% ($n = 22$) in the oldest patches. The low densities of both species in older patches was not associated with low productivity, suggesting that habitat selection occurred independently of potential productivity in this novel habitat. *Received 21 June 1996, accepted 10 February 1997.*

LANDSCAPE MODIFICATION can have various effects on bird populations. For example, habitat loss may reduce overall population size (Lynch and Whigham 1984) and decrease population resilience after stochastic events (Freemark and Merriam 1986). Habitat fragmentation has the potential to create source/sink dynamics that cause independent populations to become dependent on source populations (Pulliam 1988). Edge effects can increase nest predation for passerines (Wilcove 1985, Paton 1994, Yahner and Mahan 1996), thus creating ecological traps (Gates and Gysel 1978, Ratti and Reese 1988, Terborgh 1992). Most studies of the effects of landscape modification on birds have focused on species in fragmented original habitat, rather than on species colonizing the newly created habitat.

Clearcuts in mature forest increase the frequency of early seral stages in the landscape. Forest management may mimic forest landscape patterns traditionally produced in fire-dominated ecosystems (Bunnell and Kremsater 1990). Species that naturally inhabit burns may colonize clearcuts as an alternate habitat because the role of fire has been reduced or eradicated in many forest regions (Hutto 1995). However, habitats such as clearcuts may superficially resemble traditional habitats but differ in subtle attributes (Bunnell and Kremsater 1990) that can influence population demography (e.g. Zwickel and Bendell 1972, Dunning and Watts 1990).

Habitat quality cannot always be assessed from population density because reproductive success can differ independent of density (Van

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Horne 1983, Vickey et al. 1992). In particular, species may be poorly adapted to a novel or modified environment. An understanding of individual habitat selection decisions and the subsequent fitness consequences associated with these decisions is necessary to assess the potential influence of habitat modification on individuals, populations, and ultimately on biodiversity (Martin 1992).

Habitat selection in variable environments has been modeled under various assumptions; in particular the Ideal Free Distribution (Fretwell and Lucas 1970), the Despotic Distribution (Fretwell and Lucas 1970, Fretwell 1972), and the Pre-emptive Model (Pulliam 1988, Pulliam and Danielson 1991). An assumption common to these models is that the observed distribution of individuals has a density-dependent component. Interpretation of the distribution of individuals in newly created habitats requires knowledge of whether the population density approaches carrying capacity. If the habitat is not saturated, then all individuals may occupy good habitat. At high population density, however, some individuals may occupy lower-quality habitat. The presence of nonbreeding "floater" males has been demonstrated in many bird populations (Brown 1969, Martin 1989) and implies that breeding population size is limited by a shortage of females and/or territories. However, the demonstration of floaters of both sexes, necessary to infer habitat saturation, has been demonstrated less often (Power 1975, Hannon and Zwickel 1979, Village 1983, Stutchbury and Robertson 1985).

We studied habitat selection and productivity of two secondary cavity nesters, the Mountain Bluebird (*Sialia currucoides*) and the Tree Swallow (*Tachycineta bicolor*), that colonized clearcuts in British Columbia. Cavity-nesting birds often are limited by availability of suitable nest sites (Scott 1979, Brawn and Balda 1988, Newton 1994), and secondary cavity-nesters may be particularly vulnerable because they are unable to excavate their own cavities. Nest-site limitation may be a particular problem in plantation forests, where suitable "wildlife trees" (mature dead or dying trees) often are targeted for removal (Hunter 1990). Additionally, cavity nesters may be limited by habitat preferences (Welsh and Capen 1992) and competition (Rosenzweig 1985). Nest-site selection by secondary cavity nesters cannot be assessed solely by observed cavity use, because natural cavities may be unevenly distributed in the environment and may vary in quality. Accordingly, we added nest boxes to 15 clearcut patches in order to standardize the availability, distribution, and quality of nesting sites. Using data from natural cavities and nest boxes, we tested: (1) preferences for, and productivity differences between natural cavities and nest boxes; (2) factors limiting breeding density for species colonizing this novel habitat; (3) proximate factors influencing selection among patches of different ages and within individual patches; and (4) the overall demographic consequences of habitat selection and nest-site preferences.

STUDY AREA AND METHODS

Study site.—The study site was in the Beaverfoot Valley in the Rocky Mountains southeast of Golden, British Columbia (50°N, 116°W, 1,400 m elevation; Fig. 1). The valley originally comprised contiguous montane spruce forest (white spruce [*Picea glauca*], Engelmann spruce [*P. engelmannii*], and hybrids) and lodgepole pine (*Pinus contorta*), with a fire-dominated ecology. Logging began in 1968 and continues to the present time, resulting in a mosaic of 70 clearcuts (10 to 85 ha each) surrounded by mature forest (Fig. 1). Most of the clearcuts have been replanted and are at various stages of regeneration, ranging from bare patches (logged in 1993) to stands of 4-m-tall lodgepole pine and hybrid spruce.

The cavity-nesting assemblage.—The clearcuts were colonized by two species of primary cavity nesters (Northern Flicker [*Colaptes auratus*] and Hairy Woodpecker [*Picoides villosus*]) and four species of secondary cavity nesters (Mountain Bluebird, Tree Swallow, Black-capped Chickadee [*Parus atricapillus*], and Boreal Chickadee [*P. hudsonicus*]). Both primary cavity nesters occurred in low numbers, with approximately 15 pairs of each species in the study area. Most of the natural cavities in the Beaverfoot were excavated by Northern Flickers (50% of 42 natural cavities used during the study) and Hairy Woodpeckers (7%) in low stumps (0.3 to 2 m) created by winter logging. Northern Flickers and Hairy Woodpeckers also excavated cavities in aspen (14%) at heights between 3 m and 12 m. We could not determine the origin of 17% of the excavated cavities. Natural holes created by fire in the center of tree stumps (12%) were 0.3 to 1 m high and were used for nesting only by Mountain Bluebirds. Two species of mammals used the boxes or cavities (deer mouse [*Peromyscus maniculatus*] and northern flying squirrel [*Glaucomys sabrinus*]).
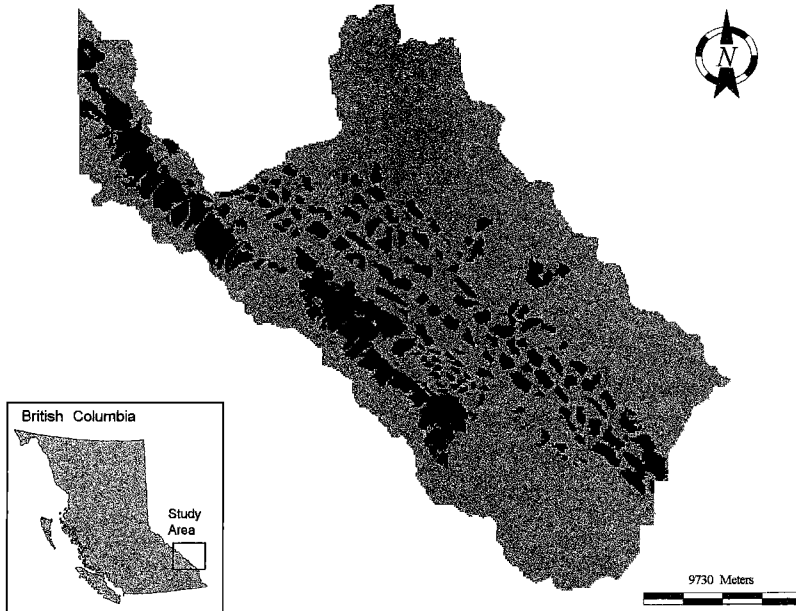
FIG. 1.   Satellite image of the Beaverfoot Valley study area in the Rocky Mountains, British Columbia. Clearcut patches 3 to 27 years old are highlighted.

Mountain Bluebirds.—Mountain Bluebirds arrived on the study area in late April, males about a week before females. We found nests by observing pairs and by systematically checking cavities and boxes. In 1993, data collection began late in the season, and we were unable to determine whether nests were first attempts or renests. The status of 86% of 121 nests in 1994 and 1995 was known because new pairs were discovered before the onset of laying. We checked nests every three days to determine clutch initiation, clutch size, nest fate, fledging dates, and chick production, using either a flashlight and a dental mirror (for deep cavities) or a small mirror attached to a stick (for high boxes). All nest boxes and most of the natural cavities were checked, but data were not obtained for 11 natural nests (25%) that were inaccessible due to nest height or tree instability. Arrival dates of bluebirds were similar in 1994 and 1995. The incubation period was 12 days, and chicks left the nest after 18 to 21 days (see Power and Lombardo 1996). Adults were captured in a nest trap designed by R. F. Holt. We banded 68 adults and 130 chicks with Canadian Wildlife Service numbered aluminum leg bands and a unique combination of two colored leg bands.

Tree Swallows.—Tree Swallows arrived in the Beaverfoot Valley in the first week of May, 7 to 14 days later than bluebirds. They initially remained in flocks and examined many potential nesting sites. Nest building generally began about a week before clutch initiation, and no pairs attempted a second clutch.

Chicks spent 18 to 22 days in the nest, and were fed by both parents. We checked swallow nests with the same protocol used for bluebird nests.

Habitat description.—We classified patches (clearcuts) into four categories: "very open," "open," "treed," and "young forest." Very open patches ($n = 10$) had no vegetation more than 1 m tall and mostly were covered with shrubs (but with patches of grass and bare ground). Open patches ($n = 30$) were dominated by low vegetation (forbs and shrubs), but with up to 20% cover of trees 1 to 3 m high. Treed patches ($n = 21$) had a predominant cover of young trees (40 to 70%) between 1 and 3 m high. Young forest patches ($n = 5$) were comprised predominantly of conifers 3 to 4 m high. We recorded vegetation characteristics in each patch along two parallel transects 150 m long and 75 m apart. Transects were adjacent to nest boxes, or natural cavities where possible, or were placed randomly in the patch if no cavities were present. Along the entire length of each transect, we recorded the predominant vegetation covering each 1-m square ($\pm$ 5%). Categories measured were: bare ground, forbs and grasses, shrubs, saplings <1 m tall, saplings 1 to 2 m tall ("medtree"), and trees >2 m ("talltree"). Arcsine transformation was used to normalize proportional data, and factor analysis was used to determine the principal vegetation variables and to reduce the number of variables if possible. The first three factors explained 98.7% of the variance in the data. Factor 1 explained 44.7% of the variance and was made up of forb (varimax rotated fac-

tor loading = −0.94) and talltree (varimax rotated factor loading = 0.92). Factor 2 (medtree) explained 27.2% of the variance and had a rotated factor loading −0.98, and Factor 3 (shrub) explained 27.9% of the variance and had a rotated factor loading of −0.98. The other two categories, bare ground and small trees, were insignificant and were dropped from further analyses. The rotated factor loadings and correlation analyses indicated that forb and tall trees were highly negatively correlated ($r^2 = -0.79$, $n = 38$, $P < 0.0001$). Because the talltree variable probably has more relevance to perching insectivorous birds than does the forb variable, we dropped forb from further analyses. Both medtree and shrub were negatively correlated with talltree, so these data were not used directly in further analyses (see Zar 1984). However, the residuals of the regressions between talltree/shrub and talltree/medtree were uncorrelated with the original talltree data and were used in further analyses as representation of factors 2 and 3.

In all further discussion, we use "patch age" as an equivalent for "patch successional age," and the categories represent increasing successional ages from very open to young forest. We used a categorical experimental design to address questions of patch occupation and variations in breeding success in relation to patch age. We used the variables talltree, and residuals of medtree and shrub, to predict occupation and density of pairs in patches using discriminant function and multiple regression analyses. Statistical analyses were performed using Systat version 5.0 (1992).

Experimental design.—Prior to the 1994 breeding season, eight nest boxes were added to each of five experimental patches in each of three patch-successional age categories (very open, open, and treed), giving a total of 15 experimental patches. In 1995, boxes were added to another four patches unoccupied in 1993 and 1994 in the young forest category to determine whether pairs would be excluded from nesting in this older successional stage. To determine whether floaters were present, we added eight boxes to four patches that were unoccupied in 1993 after the initiation of first clutches in both 1994 and 1995.

To address nest-site preferences and variation in offspring production within patches, four boxes were placed on the edge and four in the interior of each patch, with two boxes placed 1.5 m above ground and two placed 3 m above ground. We used 1.5 m for low boxes because this was the median height of natural cavities excavated in stumps on the study area, and 3 m for high boxes because this was the tallest box we could easily erect and then monitor in large numbers. We erected a total of 120 boxes, with 60 placed in the interior and 60 on the edge of patches. Half of each category was placed high and the other half was placed low. Boxes were placed 75 m apart based on mean nearest-neighbor distance

for high densities of Eastern Bluebirds (*Sialia sialis*; Gowaty and Bridges 1991). To standardize the position of interior boxes in patches of variable size, the corner box was placed 75 m from the patch edge in all patches. The cavity entrance diameter was 62 mm, which was the median diameter for natural cavities in the study area in 1993 (Holt 1997). Throughout the study, we monitored use of natural cavities by both species.

RESULTS

Natural cavities versus nest boxes.—Despite the presence of nest boxes, the number of birds of both species that nested in natural cavities did not change during the study; however, use of nest boxes increased with increasing density of boxes (Table 1). For Mountain Bluebirds, initiation dates for first clutches were statistically equal for nests in boxes and natural sites (nested ANOVA, $F = 0.81$, df = 1 and 48, $P = 0.37$), suggesting that bluebirds did not prefer one nest type over the other. We could not conduct a similar analysis for Tree Swallows because only five pairs of swallows nested in natural cavities in each year.

Measures of reproductive success did not differ between natural cavities and nest boxes, pooled across years (clutch size: $\bar{x} = 5.3 \pm$ SE of 0.1 in boxes and in cavities, $n = 23$ for each; number young fledged from successful nests: $\bar{x} = 4.7 \pm 0.4$, $n = 12$ in boxes vs. $\bar{x} = 4.8 \pm 0.5$, $n = 13$ in natural cavities). Because nest boxes did not differ from cavities in preference or in reproductive success, we combined data in subsequent analyses where appropriate.

Nest-site availability and patch age.—The distribution of natural cavities was uneven with respect to patch age. Most of the cavities were in open and treed patches, with only a few in young forest patches and none in very open patches (Table 1). In 1993, prior to the addition of nest boxes, the distribution of the 23 Mountain Bluebird and 5 Tree Swallow pairs largely reflected the distribution of natural cavities (Table 1). During 1994 and 1995, the number of bluebird and swallow pairs increased following nest-box addition, and the distribution of these pairs expanded in relation to patch age (Table 1). Both species occupied very open patches only after the addition of nest boxes, and the number of bluebird and swallow nests increased two-fold and almost eight-fold, respectively, in the open patches. Density also in-

TABLE 1.   Number of pairs of Mountain Bluebirds and Tree Swallows, and number of clearcut patches with nesting cavities (natural or nest box) in relation to seral stage and year. Patches increase in age from very open to young forest.

| | Seral stage (patch age)[a] | | | | | | | | |
| | Experimental patches | | | | Non-experimental patches | | | | |
Year	Very open	Open	Treed	Young forest	Very open	Open	Treed	Young forest	Total no. pairs
				Mountain Bluebird					
1993	0	0	0	0	0	19	4	0	23
1994	5	6	3	0	0	15	3	0	32
1995	5	6	5	0	0	18	6	0	40
				Tree Swallow					
1993	0	0	0	0	0	3	2	0	5
1994	6	8	6	0	0	2	2	0	24
1995[b]	14	14	8	2	0	3	1	0	42
				No. of patches with nest site					
1993	0	0	0	0	0	22	11	4	—
1994	5	5	5	0	0	22	11	4	—
1995	5	5	5	4	0	22	11	4	—

[a] Experimental patches contained nest boxes in 1994 and 1995; non-experimental patches contained natural cavities only.
[b] Distribution of Tree Swallow nests varied significantly with patch age (see text).

creased in treed patches, although not all patches were occupied (Table 1). Only Tree Swallows occupied boxes in young forest patches in 1995, and they did not occupy all available patches (Table 1). In both 1994 and 1995, the distribution of bluebird pairs did not differ from that expected if pairs showed no preference for patch age (both years: Kolmogorov-Smirnov test, $d_{max} = 1$, $n = 14$, $P > 0.5$). In 1994, Tree Swallow distribution did not differ from the null hypothesis of no preference for patch age ($d_{max} = 1$, n 20, $P > 0.05$). In 1995, however, swallow distribution varied with

patch age ($d_{max} = 9$, $n = 36$, $P < 0.01$), with a higher frequency of pairs in very open and open patches, and a lower frequency than expected in treed and young forest patches (Table 1).

Patch sharing and intraspecific competition.— Numbers of both species increased with the addition of nest boxes, but within experimental patches only 23% (1994) and 25% (1995) of the original 60 boxes were occupied by Mountain Bluebirds (Table 2). In 26 of 28 occupied experimental patches (over two years), only one bluebird pair occupied each patch at one time (Ta-

TABLE 2.   Fecundity measures ($\bar{x} \pm SE$, n in parentheses) and experimental box occupation patterns (no. of boxes occupied, no. available in parentheses) for Mountain Bluebirds and Tree Swallows.

| | Mountain Bluebird | | Tree Swallow | |
	1994	1995	1994	1995
	Fecundity measures			
Mean date of first egg	12 May	19 May	11 June	11 June
Clutch size	5.5 ± 0.14 (13)	4.9 ± 0.25 (14)	5.2 ± 0.22 (17)	5.2 ± 0.06 (19)
Chicks fledged/pair[a]	4.6 ± 0.37 (8)	4.8 ± 0.26 (7)	4.7 ± 0.43 (12)	4.6 ± 0.86 (8)
Second clutches (%)[b]	4 (32)	0 (40)	0 (24)	0 (40)
	Experimental box occupation			
No. of edge boxes	0 (60)	0 (60)	0 (60)	0 (60)
No. of interior boxes	13 (60)	16 (60)	20 (47)	36 (44)
No. of high boxes	7 (30)	8 (30)	15 (23)	22 (22)
No. of low boxes	6 (30)	8 (30)	5 (24)	14 (22)

[a] For nests that fledged at least one chick.
[b] Proportion of pairs renesting after a successful first brood.

TABLE 3. Intraspecific patch sharing by Mountain Bluebirds and Tree Swallows in patches with nest boxes added (experimental) and patches with natural cavities only (non-experimental). Data are number of patches occupied by the number of nesting pairs indicated in boxhead (i.e. 0, 1, 2, etc.).

	No. of pairs in experimental patches					No. of pairs in non-experimental patches			
Year	0	1	2	3	4	1	2	3	4 to 6
Mountain Bluebird									
1993	—	—	—	—	—	7	0	0	1
1994	2	12	1	0	0	5	3	0	1
1995	0	14	1	0	0	11	2	0	1
Tree Swallow									
1993	—	—	—	—	—	2	0	0	0
1994	2	7	5	1	0	4	0	0	0
1995	0	1	7	7	0	5	0	0	0

TABLE 4. Summary of intraspecific patch sharing by Mountain Bluebirds and Tree Swallows. Only patches with multiple nest sites are included. Sample size (total number of patches that could have contained >1 pair or number of pairs nesting in patches with >1 nest site available) is shown in parentheses.

Year	No. of patches with >1 pair	%	No. of pairs sharing a patch	%
Mountain Bluebird				
1993	1 (8)	12	6 (13)	46
1994	5 (24)	20	13 (30)	43
1995	4 (29)	14	12 (37)	32
Tree Swallow				
1993	0 (2)	0	0 (2)	0
1994	6 (19)	31	13 (24)	54
1995	14 (20)	70	35 (41)	85

ble 3). We tested the goodness of fit of the observed distribution of patch occupation against a Poisson distribution (Zar 1984). In 1994 and 1995, the bluebird distribution differed from random (1994: $G = 11.83$, $df = 1$, $P < 0.001$; 1995: $G = 11.9$, $df = 1$, $P < 0.001$). The population mean and variance in both years showed that the observed distribution was more dispersed than random. A different pattern of patch sharing was observed in the non-experimental patches (Table 3). In patches with multiple nest sites, most were occupied by a single pair of bluebirds. However, three patches were occupied by two pairs of bluebirds, and one patch had five and six pairs nesting in close proximity in natural cavities in 1994 and 1995, respectively (Table 3).

Tree Swallows occupied 43% of the 47 boxes left unoccupied after bluebird settlement in 1994 (Table 2). The distribution of swallow nests differed from random in 1994 ($G = 6.0$, $df = 2$, $P < 0.05$), and comparison of the population mean and variance showed that nests were more dispersed than random. In 1995, swallows occupied 81 % of the remaining boxes, effectively saturating the habitat evenly.

We examined the influence of intraspecific competition on patch occupation as: (1) the number of patches occupied by more than one pair of each species, and (2) the proportion of the total number of nesting pairs of that species that shared a patch with one or more pairs (Table 4). Because bluebirds and swallows were

nest-site limited, the analysis included only 15 experimental and 14 non-experimental patches with multiple nest sites occupied at least once during the study. The percentage of patches shared by Mountain Bluebird pairs remained relatively constant over the three years ($\bar{x} = 15 \pm 2\%$; Table 4). The percentage of pairs sharing patches also was relatively constant ($\bar{x} = 40 \pm 4\%$; Table 4). Both the percentage of Tree Swallow pairs sharing patches and the percentage of shared patches increased over the study period (Table 4).

The median patch size in the study area was 22 ha. Patches with a single bluebird pair did not differ in size ($\bar{x} = 27 \pm 61$ ha) from patches with more than one pair ($\bar{x} = 26.2 \pm 88$ ha). Considering only patches that contained more than one nest, patch size was not correlated with the maximum number of pairs observed in a patch (Mountain Bluebird: $r_s = 0.08$, $n = 30$, $P > 0.50$; Tree Swallow: $r_s = -0.26$, $n = 15$, $P > 0.20$).

Nonbreeding floaters.—To determine whether nonbreeding Mountain Bluebirds inhabited the study area, we added nest boxes to four previously unoccupied patches in 1994 and 1995 after for all known Mountain Bluebird pairs had started incubating. All four patches were occupied in 1994 (one bluebird pair per patch), and 50% of patches were occupied within six days in 1995 (one pair in each of two patches). All of the new pairs were unbanded, and no pair disappeared from known nesting sites during this period. Therefore, we assume that

these birds constituted a floater population that would not have nested if the extra boxes had not been available. This experiment could not address whether the Tree Swallow population was saturated, because most of the swallows had not started laying when the experiment was conducted.

Proximate factors limiting breeding density.— Analysis of nest-box occupation in relation to patch age suggested that settlement in experimental patches was nonrandom (Table 1). Based on discriminant function analysis of vegetation structure within occupied versus unoccupied patches, the most important predictor of patch occupation by Mountain Bluebirds was the talltree variable. The shrub and medium tree variables were not significant predictors of occupation (univariate tests: talltree $F = 22.9$, df = 1 and 36, $P < 0.0001$; medtree: $F = 1.8$, df = 1 and 35, $P = 0.18$; shrub: $F = 0.002$, df = 1 and 36, $P = 0.9$). The overall model was significant (Wilks' lambda = 0.56, $F = 8.8$, df = 3 and 34, $P < 0.001$), and it correctly classified the occupation status for 92% of the patches.

Tree Swallows occupied almost all of the experimental patches, so we could not compare occupied versus unoccupied patches. However, density of swallows varied among patches, allowing us to examine the relationship between pair density and vegetation in a multiple regression. We used maximum Tree Swallow density as the factor variable to avoid sampling the distribution before saturation. Tree Swallow density was affected by vegetation (multiple $r = 0.72$, $F = 6.16$, df = 3 and 17, $P < 0.005$); specifically, it was inversely related to the tall tree variable (partial $r = -0.65$, $t = -4.3$, $P < 0.001$). Shrub and medium tree variables were unrelated to Tree Swallow density, and swallow density was predicted accurately using only the tall tree variable in the overall model.

Four interior boxes and four edge boxes were available in each experimental patch. Mountain Bluebirds and Tree Swallows occupied only interior boxes in both years (Table 2). Of the 60 interior boxes, pairs could choose between an equal number of high and low boxes. Stratifying data by years (Table 2), occupation of boxes by Mountain Bluebirds was unaffected by box height ($\chi^2 = 0.05$, df = 1, $P = 0.83$), whereas Tree Swallows were more prevalent in high boxes ($\chi^2 = 17.7$, df = 1, $P < 0.0001$). In 1994, six patches had only single pairs of swallows

and one pair of bluebirds, presumably giving bluebirds a free choice of box height. Again, bluebirds exhibited no preference for box height ($\chi^2 = 0.2$, df = 1, $P = 0.63$), although our sample size was small.

Clutch and brood size.—Considering Mountain Bluebirds nesting in experimental patches, mean clutch size and the mean number of fledglings from successful nests did not vary between years (two-way ANOVA; clutch size: $F = 1.68$, df = 1 and 21, $P = 0.21$; fledglings: $F = 0.24$, df = 1 and 11, $P = 0.63$) or among patches of different ages (clutch size: $F = 1.16$, df = 2 and 21, $P = 0.33$; fledglings: $F = 0.24$, df = 1 and 11, $P = 0.63$; Table 5). Mean clutch size and mean number of chicks fledged also did not vary with year (clutch size: $F = 0.07$, df = 1 and 29, $P = 0.79$; fledglings: $F = 0.11$, df = 1 and 14, $P = 0.75$) or patch age (clutch size: $F = 0.39$, df = 2 and 29, $P = 0.68$; fledglings: $F = 0.31$, df = 2 and 14, $P = 0.74$; Table 5) for Tree Swallows. There were no significant year and patch-age interactions.

Clutch initiation date.—The timing of clutch initiation could be influenced by traits of nesting birds or by external factors such as date of snow melt or habitat quality. To determine whether clutch initiation date was independent in individual patches across years, we tested for a correlation between initiation dates within patches in 1994 and 1995. Clutch initiation dates were not correlated between years in Mountain Bluebirds ($r_s = 0.09$, $n = 13$, $P > 0.50$) or in Tree Swallows ($r_s = 0.20$, $n = 16$, $P > 0.20$). We then used a two-way ANOVA to determine that clutch initiation date in Mountain Bluebirds was not significantly affected by either year or patch age (year: $F = 2.98$, df = 1 and 25, $P = 0.09$; patch age: $F = 2.22$, df = 2 and 25, $P = 0.13$). Clutch initiation dates of Tree Swallows also did not vary with year ($F = 0.07$, df = 1 and 38, $P = 0.78$), but they did vary with patch age ($F = 8.57$, df = 2 and 38, $P = 0.001$; Table 5). This difference was due to the later clutch initiation of clutches in very open compared with the open ($P = 0.0001$) and treed ($P = 0.04$) patches (Tukey tests). Interactions between year and patch age were not significant for either species.

Nest predation and productivity.—Because nest predation rates may be influenced by nest height, we classified natural cavities into low (<3 m) and high (>3 m) nests. The proportion

TABLE 5. Mountain Bluebird and Tree Swallow fitness correlates, in relation to patch-age category. Data are $\bar{x} \pm$ SE, with sample size in parentheses.

	Mountain Bluebird			Tree Swallow		
	Very open	Open	Treed	Very open	Open	Treed
Clutch initiation date	12 May ± 1.7 (10)	15 May ± 1.7 (10)	18 May ± 1.6 (11)	18 June ± 2.2 (12)	6 June ± 1.1 (19)	11 June ± 3.0 (12)
Clutch size	5.5 ± 0.29 (7)	4.9 ± 0.26 (9)	5.2 ± 0.23 (11)	5.4 ± 0.42 (7)	5.2 ± 0.26 (18)	4.9 ± 0.35 (10)
No. chicks fledged	—	4.8 ± 0.26 (7)	4.6 ± 0.37 (8)	5.2 ± 0.96 (4)	4.9 ± 0.67 (8)	4.6 ± 0.67 (7)
Predation rate 1994[a]	80 (5)	20 (5)	0 (3)	75 (4)	25 (8)	16 (6)
Predation rate 1995[a]	100 (5)	40 (5)	40 (5)	93 (15)	57 (7)	43 (7)
Potential productivity[b]	0.65 ± 1.45	3.6 ± 2.2	4.0 ± 1.4	0.85 ± 1.6	3.0 ± 2.3	3.6 ± 2.1

[a] Percent of nests depredated; data from nest boxes only.
[b] Potential productivity (no. chicks per pair) is estimated using a deterministic model based on mean clutch size and the mean predation probability observed in 1994 and 1995 for each patch-age category.

of nests depredated did not differ by height (two-way ANOVA; $F = 0.003$, df = 1 and 2, $P = 0.96$) or by year ($F = 1.55$, df = 2 and 2, $P = 0.39$). Predation rates at high and low nest boxes also did not vary with height class ($F = 0.001$, df = 1 and 1, $P = 0.99$) or with year ($F = 0.04$, df = 1 and 1, $P = 0.87$). Including only experimental patches, predation rate did not differ between species (three-way ANOVA; $F = 0.98$, df = 1 and 5, $P = 0.37$), but did differ with patch age ($F = 41.99$, df = 2 and 5, $P = 0.001$) and year ($F = 12.75$, df = 1 and 5, $P = 0.02$; Table 5). Predation rates were higher in very open compared with open ($P = 0.008$) and treed ($P = 0.001$) patches (Tukey tests; Table 5). We estimated potential productivity using mean clutch size for each species and mean predation probability in each patch-age category. Potential productivity was 2.5 to 3.5 chicks per pair lower in the very open compared with the older patches (Fig. 2, Table 5).

DISCUSSION

Nest-site availability and patch succession.— Nest-site availability often limits secondary cavity nesters (Lack 1954, Scott 1979, Brawn and Balda 1988, Newton 1994; but see Welsh and Capen 1992). In our study area, the lack of cavities precluded Tree Swallows and Mountain Bluebirds from nesting in young patches and limited breeding densities in mid-age patches. Vegetation structure may determine avian species presence and composition (James 1971, Anderson and Shugart 1974, Martin 1992, Hansen et al. 1995), and both species disappeared from our study area after more than 20 years of vegetational succession, despite the presence of available nest sites. Patch occupation may be related to a number of factors, including changes in prey abundance or availability with vegetation structure and variation in the probability of predation (Yahner and Mahan 1996).

Patch occupation and patch sharing.—Bluebirds occupied about 90% of the available experimental patches, but less than 15% of the pairs nested concurrently with conspecifics, resulting in a "one pair per patch" pattern. The presence of floaters suggested that bluebirds sometimes defer breeding rather than nest in close proximity to conspecifics. Floater pairs can be present despite the availability of apparently
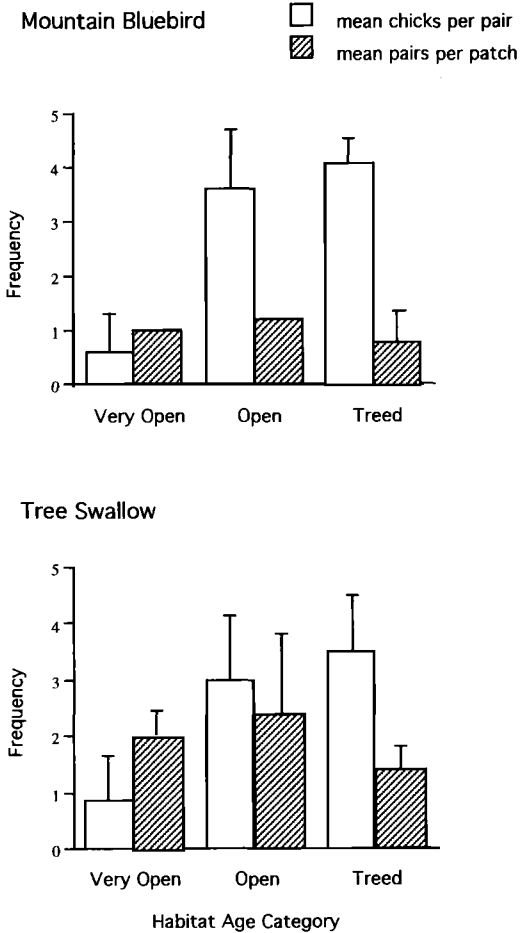
Mountain Bluebird   □ mean chicks per pair
                      ▨ mean pairs per patch

Tree Swallow

Habitat Age Category

FIG. 2. Potential productivity (± SE) and mean number of pairs per patch for Mountain Bluebirds and Tree Swallows in relation to successional age of patches.

suitable habitat (Power 1975, Stutchbury and Robertson 1985). At low density, swallows were over-dispersed, but both the percentage of pairs sharing a patch, and the percent of patches shared, increased throughout the study. Muldal et al. (1985) also observed Tree Swallows spacing themselves throughout clusters of nest boxes, but intrapair distances decreased when density increased. Nesting dispersion also was observed in Eastern Bluebirds that nested with a mean nearest-neighbor distance of 70 m, even though boxes were 30 m apart (Gowaty and Bridges 1991). Tree Swallows occasionally nest 1 to 2 m apart (Harris 1979), although 15 m is a more common distance (Rendell and Robertson 1990).

The existence of floaters allowed us to interpret the observed distribution patterns with more confidence. For instance, in occupied patches bluebird pairs were over-dispersed rather than uniformly distributed, which simply may be a function of low pair density. However, the presence of floater pairs strengthens the possibility that intraspecific competition limited the nesting density of bluebirds. Floater pairs have previously been demonstrated experimentally for Mountain Bluebirds (Power 1975), and in many amateur nest-box programs bluebird densities increase immediately after the addition of nest boxes (Newton 1994). Floater pairs may be a general phenomenon in populations that are nest-site limited.

Behavioral avoidance of conspecifics is much stronger for bluebirds, perhaps limiting bluebird density at low levels, whereas swallow density increased until the available boxes were saturated. The different response in density between these otherwise similar species stresses the importance of including species-specific life-history information in models that aim to assess the implications of resource management on biodiversity (Westman 1990, Hansen and Urban 1992, Hansen et al. 1992).

Nest-site selection.—Our experimental design allowed pairs to choose between boxes placed on the edge versus the interior of clearcut patches. Although both species appeared to be limited by the availability of nest sites, neither species occupied boxes on the edge of experimental patches. Rendell and Robertson (1990) also found that Tree Swallows avoided edge habitat. They explained this behavior as an avoidance of interference from House Wrens (*Troglodytes aedon*), which nest preferentially within 30 m of the forest edge. In the same study, however, 69% of Eastern Bluebirds nested within 30 m of the edge and presumably also lost nests to House Wrens. Unlike other studies (Zarnowitz and Manuwal 1985, Rendell and Robertson 1990, Li and Martin 1991), our cavity-nesting assemblage had low species diversity and presumably had lower levels of interspecific competition for nest sites. An alternative explanation for avoidance of edges is nest-predation avoidance. Predator abundance may increase at forest edges (see Paton 1994), and both species may avoid the forest edge as a result of predation risk.

Height of nest cavity affects nesting success

in some cavity-nesting birds, apparently because of the increased predation in low nest sites (Nilsson 1984, Li and Martin 1991). In our experimental design, birds could choose between boxes 1.5 and 3 m above ground. Mountain Bluebirds showed no preference for nest-box height within this range. Tree Swallows, however, clearly preferred high boxes, and all natural cavities used by nesting swallows were in high stumps (>3 m) or standing aspens (>4 m). The shortage of natural cavities high in trees may explain the small number of nesting swallows before boxes were available. We have no evidence that predation differed between low and high boxes, or between low and high natural cavities. The height range in our study, however, may have been insufficient to deter predators even if nests higher than 3 m were less vulnerable than lower nests.

Habitat selection and consequences for reproductive success.—Habitat selection has important fitness consequences and therefore is expected to be under strong selection (Cody 1985). Theories that relate habitat-selection decisions to habitat quality and conspecifics have assumed that individuals have a good knowledge of their habitat and can assess risk (Fretwell and Lucas 1970, Pulliam and Danielson 1991). Fecundity of both Mountain Bluebirds and Tree Swallows did not vary with patch age, but productivity was highly skewed as a result of high nestling predation in young patches. Nevertheless, both bluebirds and swallows nested in the young patches at least as frequently as in older patches. This result is inconsistent with our expectation that individuals should optimize fitness. One explanation is that patterns of patch occupation are age specific. Young or less-experienced birds may be more prevalent in the very open habitat, consequently lowering productivity in these patches (Wheelwright and Schultz 1994, Martin 1995). Tree Swallows initiated clutches later in very open than in older patches, which gives tentative support for this hypothesis. However, we also used artificial eggs to examine patterns of nest predation in the study area, which effectively controlled for variation in adult quality. Results from these experiments showed similar patterns of nest predation with patch age (Holt 1997), suggesting that the patterns we observed did not result from age-related phenomena.

Another explanation is that pairs in very

open habitat simply are making "the best of a bad job" (sensu Krebs and Davies 1987), with the alternative being to forego nesting or to nest in a patch with conspecifics. We cannot reject this hypothesis, although it seems unlikely that the cost of patch sharing exceeds that of an 87% nest-predation rate. Additionally, it is possible that data obtained from birds nesting in nest boxes does not reflect natural predation rates. In our study, nest boxes were similar in height and cavity diameter to most of the natural cavities in the area, which was reflected in the similar predation rates observed in these two types of nests (Holt 1997). The most parsimonious explanation of the apparent dilemma between patch occupation and potential fitness is that these birds had no *a priori* knowledge of predation risk in this novel habitat and thus did not include predation costs in their habitat assessment.

Published examples of species that apparently are poorly adapted to their environment are scarce. In a study of nest-site selection and nest predation in small drainages on the Colorado Plateau, Hermit Thrush (*Catharus guttatus*) and MacGillivray's Warbler (*Oporornis tolmiei*) nests in small firs had lower reproductive success (owing to high nest predation) than nests in surrounding vegetation (Martin and Roper 1988, Martin 1993). For both species, small firs may be more appropriate nesting sites in other parts of their range, and although they conferred low reproductive success on the Colorado Plateau, their use may be maintained by birds originating from areas where the behavior results in high reproductive success (Martin 1993). A similar phenomenon may be occurring with Mountain Bluebirds and Tree Swallows colonizing the novel habitat created by clearcutting. Both species seemed well adapted to colonizing transient habitats, but neither species appeared to adjust patch-selection decisions to encompass variation in the patterns of nest predation.

Traditionally, Mountain Bluebirds and Tree Swallows inhabit open habitats such as farmland, parkland, and ephemeral open areas produced after fires (Zeleny 1976). Bluebird populations in North America declined in the early half of this century, apparently as a result of large-scale removal of suitable trees and stumps for nesting (Zeleny 1976, Newton 1994) as well as competition with introduced Euro-

pean Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*). Nest-box trails were initiated to counter this decline and appear to have been successful in many areas (Kibler 1969, Backhouse 1986, Robertson et al. 1992, Power and Lombardo 1996). More recently, bluebirds and Tree Swallows, as well as primary cavity nesters, have colonized clearcuts (Conner 1974, Bennett 1994), and many studies have suggested methodologies to increase the numbers of cavity nesters in clearcuts (e.g. Conner 1978, Schreiber and deCalesta 1992, Bennett 1994). However, the demographic consequences of nesting in clearcuts are uncertain. The overall high predation rates that we found suggest that the Beaverfoot Valley is less productive than it might initially appear, and it probably is less productive than most traditional habitats. However, the net effect of creating patches of early seral stages may be positive for these species. Mountain Bluebirds and Tree Swallows produced offspring in the study area, despite high rates of nest predation. The net effect of newly created clearcuts on the population dynamics of these species will depend on whether less-productive areas are colonized in addition to (or as an alternative to) more productive traditional habitats.

We have demonstrated that breeding densities of cavity nesters are limited by a hierarchy of species-specific factors, including nest-site availability, vegetation structure, and intraspecific competition. Consequently, the addition of nest sites to managed landscapes will not necessarily result in global increases of all cavity nesters. Management strategies should consider variation in species-specific traits to determine the placement and physical attributes of wildlife trees (e.g. snags) necessary to maintain productivity in a forest matrix. The life-history consequences of wildlife reserve patches and snags for cavity-nesting species should be evaluated before embarking on ambitious and perhaps counterproductive wildlife enhancement in managed forests.

ACKNOWLEDGMENTS

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