NEST-SITE SELECTION AND NESTING SUCCESS OF CAVITY-NESTING BIRDS IN HIGH ELEVATION FOREST DRAINAGES

PINGJUN LI[1,3] AND THOMAS E. MARTIN[2]

[1]Department of Zoology, Arizona State University, Tempe, Arizona 85287 USA, and
[2]U.S. Fish and Wildlife Service, Arkansas Cooperative Fish and Wildlife Research Unit,
Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701 USA

ABSTRACT.—We identified habitat features that characterized successful and unsuccessful nest sites, nest sites vs. random sites, and differences among coexisting species of cavity-nesting birds for 356 nests in central Arizona. Live and, more commonly, dead quaking aspens (*Populus tremuloides*) were used for 88% of all nest sites, but aspens constituted only 12% of all trees in random plots ($n = 152$). Nest patches (11.3-m-radius circle centered on the nest tree) of most bird species contained significantly more aspens and conifers, which provided foraging substrates for cavity-nesting species, than random plots, but the patches had fewer deciduous trees (except aspens). Thus, more potential nest sites and foraging substrates existed in chosen nest patches than in random plots. Failed nests generally were more concealed by foliage and were closer to conifers. Nest success was lower for species with lower nest height. Reduced nest success at lower and more concealed nests may occur because predators are more successful. Nonexcavator species had lower nesting success than excavator species possibly because they nested lower, had greater nest concealment, used older cavities, and tended to have smaller body mass. *Received 21 May 1990, accepted 26 November 1990.*

NATURAL selection favors individuals that choose resources that enhance breeding success, but limited availability of such resources can limit the number of individuals that breed. For example, availability of nest sites commonly limits populations of cavity-nesting birds (e.g. Scott 1979, Cline et al. 1980, Stauffer and Best 1982, Brush et al. 1983, Raphael and White 1984, Cody 1985, Munro and Rounds 1985). Cavities and potential sites for cavities (i.e. snags) vary in quality (as defined by reproductive success), and availability of high-quality cavities may be especially limited by competition for such sites (Nilsson 1984). Habitat features that influence site quality should be important to cavity choice and management efforts. Yet, few workers have examined nest-site characteristics that influence reproductive success (e.g. Scott 1978, Stauffer and Best 1982, Raphael and White 1984, Peterson and Gauthier 1985, Swallow et al. 1986, Gutzwiller and Anderson 1987, Runde and Capen 1987, Sedgwick and Knopf 1990, but see Nilsson 1984, Belles-Isles and Picman 1986, Finch 1989).

Quality of nest sites can be affected by microclimate, food availability, and nest predation. Cavity orientation can ameliorate microclimate effects (e.g. Reller 1972, Conner 1975, Stauffer and Best 1982, and others). Cavity-nesting birds commonly choose nests in areas where foraging substrates, such as snags and live trees, are dense (Mannan et al. 1980, Davis et al. 1983, Brush et al. 1983, Marzluff and Lyon 1983, Raphael and White 1984, Swallow et al. 1986). However, density of snags and live trees could also affect risk of nest predation. Nest predation is usually the primary source of nest mortality for both open- and cavity-nesting birds (Lack 1954; Nice 1957; Ricklefs 1969; Nilsson 1984; Martin 1988a, 1991a). As a result, choice of nest sites with reduced risk of nest predation and more foraging substrates should be favored.

Probability of predation may decrease with increasing abundance of potential nest sites (snags and cavities) because predators must search more empty sites to find an occupied site (Martin 1988c, Martin and Roper 1988). Predation risk may also increase with age of nests because older nests have a greater likelihood of previous discovery by a predator; old nests had greater rates of nest predation in Boreal Owl (*Aegolius funereus*) because predators apparently

TABLE 1. List of cavity-nesting birds and their codes, number of nests and their nesting results. Numbers in parentheses are: successful/unknown/failed.

Species	Codes	Number of nests found			
		During building	During incubating	During feeding	Total
Northern Flicker					
Colaptes auratus	NF	6 (4/2/0)	9 (9/0/0)	22 (21/1/0)	37 (34/3/0)
Red-naped Sapsucker					
Sphyrapicus varius	RS	6 (5/1/0)	7 (6/1/0)	7 (7/0/0)	20 (18/2/0)
Williamson's Sapsucker					
Sphyrapicus thryoides	WS	6 (6/0/0)	16 (14/0/2)	14 (14/0/0)	36 (34/0/2)
Hairy Woodpecker					
Picoides villosus	HW	1 (1/0/0)	2 (1/0/1)	5 (5/0/0)	8 (7/0/1)
Downy Woodpecker					
Picoides pubescens	DW	1 (1/0/0)	1 (1/0/0)	1 (1/0/0)	3 (3/0/0)
Acorn Woodpecker					
Melanerpes formicivorus	AW	3 (2/0/1)	6 (6/0/0)	4 (3/1/0)	13 (11/1/1)
Cordilleran Flycatcher					
Empidonax difficilis[a]	CF	18 (5/2/11)	14 (4/1/9)	3 (3/0/0)	35 (12/3/20)
Mountain Chickadee					
Parus gambeli	MC	7 (2/0/5)	7 (4/1/2)	15 (15/0/0)	29 (21/1/7)
White-breasted Nuthatch					
Sitta carolinensis	WN	0 (0/0/0)	4 (1/1/2)	6 (5/0/1)	10 (6/1/3)
Red-breasted Nuthatch					
Sitta canadensis	RN	6 (3/1/2)	6 (3/2/1)	2 (2/0/0)	14 (8/3/3)
Pygmy Nuthatch					
Sitta pygmaea	PN	5 (4/0/1)	4 (3/0/1)	9 (9/0/0)	18 (16/0/2)
Brown Creeper					
Certhia americana	BC	2 (1/0/1)	0 (0/0/0)	3 (3/0/0)	5 (4/0/1)
House Wren					
Troglodytes aedon	HR	53 (35/3/15)	26 (18/2/6)	41 (41/0/0)	120 (94/5/21)
Western Bluebird					
Sialia mexicana	WB	1 (0/0/1)	4 (3/0/1)	3 (3/0/0)	8 (6/0/2)
Total		115 (69/9/37)	106 (73/8/25)	135 (132/2/1)	356 (274/19/63)

[a] Eight nests without habitat data.

remembered nests raided previously (Sonerud 1985, 1989). Secondary cavity-nesting birds (nonexcavators) usually occupy old cavities abandoned by primary cavity-nesting birds (excavators) and, hence, secondary cavity-nesting birds may have higher nest mortality than primary cavity-nesting birds. Predation may also increase in lower nests (Nilsson 1984). Most predators of cavity-nesting birds in temperate environments are small mammals and tree-climbing snakes (Nilsson 1984, Sonerud 1985). These predators may be able to reach lower nests more easily and provide parent birds less time to detect and perhaps dislodge climbing nest predators (Nilsson 1984). Ability to detect and attack predators may also be reduced by dense foliage near the cavity (Belles-Isles and Picman 1986, Finch 1989). Conversely, dense foliage near nests may reduce predation by concealing the nest (reviewed in Martin 1991a). We examined these possibilities in this study.

We compared sites chosen for nesting with unused sites and compared successful with failed sites of coexisting species. We tested choice of nest sites and nesting success of coexisting species based on density of foraging substrates near the nest, nest age, nest-site availability, nest height, and foliage density at nest height.

STUDY AREA AND METHODS

Study sites.—We conducted our research on the Mogollon Rim of central Arizona (ca. 2,300 m elevation). Study sites were snow-melt drainages that contained 35 bird species, including 16 cavity-nesting species (Martin 1988b). Study sites had a mixed overstory of ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strobiformis*), quaking aspen (*Populus tremuloides*), and Gambel oak (*Quercus gambelii*). Young plants of these canopy trees, plus canyon maple (*Acer grandidentatum*) and New Mexico locust (*Robinia neomexicana*) dominated the understory woody

species (see Martin 1988b for detailed description). The drainage areas contrast with surrounding forest, which is primarily ponderosa pine with Gambel oak in the subcanopy and little understory vegetation. Nest predators for cavity-nesting birds (scientific names in Table 1) in this area included House Wrens (*Troglodytes aedon*), red squirrels (*Tamiasciurus hudsonicus*), and gray-collared chipmunks (*Tamias cinereicollis*) (Martin 1988c, pers. obs.).

Nest search and observation.—We searched 10 drainage areas in 1987, and 9 in 1988 and 1989 for nests from mid-May to mid-July. Nests were located initially by observing parents building the nest. Observations of adults entering the nesting cavity or the presence of young in the nest confirmed the location. We did not search for nests of Violet-green Swallows (*Tachycineta thalassina*) or Purple Martins (*Progne subis*).

We inspected each nest every 3–4 days. A nest was *active* if parents were observed entering the nest to incubate or feed young, *depredated* if no activity was recorded in repeated checks after activity was verified, and *successful* if parents were observed feeding young near fledging or if fledged young were observed near the nest. Some nests were classified as *unknown* because they were left unchecked. Nest success rate was calculated using the Mayfield method (Mayfield 1961, 1975) as detailed by Hensler and Nichols (1981).

Vegetation measurements.—Vegetation was sampled in an 11.3-m-radius circular plot (0.04 ha) centered either on nests (*nest patches*) or randomly chosen trees (*random plots*). A central transect was established on each drainage to select random sites (following Swallow et al. 1986). Random sites were centered on snags taller than 1.5 m and larger than 13 cm diameter breast height (DBH), which is approximately the minimum size of nest trees. The first random site was centered on the snag nearest to a point 25 m from the beginning and within 15 m of either side of the transect because approximately 85% of the nests were in these 30-m belts. Subsequent snags were chosen at least 22.6 m away and within the 30-m-wide belt. This procedure was followed until 6–10 (depending on the drainage length) nonoverlapping circular plots were defined on each transect. Approximately 30% of nests were in live aspen and so we centered approximately 30% of random plots on live aspen. Random plots were also sampled outside the 30-m belt in proportion to nest occurrence there. House Wrens had 19 nests in live maple and for these nests we located a random plot approximately 50 m away, parallel to the drainage contour, and centered on a maple stem of the same size as used for nesting.

Habitat characteristics measured in the circular plots included ground cover, shrub cover (estimated foliage cover <3 m high by woody perennials including trees <8 cm DBH), numbers and species of live stems by size classes (8–15, 15–30, 30–50, and >50 cm DBH), and numbers and species of snags by size classes (13–

20, 20–35, 35–50, and >50 cm DBH). For each snag, we recorded tree species, DBH, number of nesting cavities and indications of feeding activity.

Nest measurements.—For each active nest, we recorded (1) hole orientation (recorded in 45° octants), (2) nest height, (3) percentages of foliage cover around nest (estimated cover for 1 m² around nest entrance and within 2 m of cavity), (4) distance to the nearest coniferous tree, and (5) the bird species using the cavity. In addition, we recorded the nest-tree species, DBH, and condition of tree (snag, live with dead portion, live tree).

Statistical analyses.—We compared habitat characteristics between nest sites and random plots to evaluate choice of nest sites. Habitat characteristics were also compared among bird species to identify interspecific similarities and differences in nest sites. Because variables did not exhibit a multinormal distribution, count data were square-root transformed. All data measured as percentages and proportions were arcsine and square-root transformed.

Univariate analysis of variance (ANOVA) and stepwise discriminant function analysis were used to examine differences in habitat variables between nest and random plots (SAS 1985). In the stepwise discriminant analysis, we used the forward selection procedure with an entry criteria of 0.15. We also used these analyses to compare successful with failed nests to identify habitat variables associated with successful reproduction. We compared excavator species with nonexcavator species by nested ANOVA, where species were nested within nest type.

Cluster analysis was used to examine similarities and differences among species in nest-site selection. To improve the analysis, House Wren nests were divided into those in aspens or maples. The cluster analysis was based on Euclidean distances between mean values of habitat variables.

Daily mortalities were compared among more than two species using methods described by Sauer and Williams (1989). The relationship between average nesting success and mean nest heights, mean nest concealment, and body mass of each species was examined through multiple regression.

RESULTS

Nesting success.—We found 356 nests, including 140 in 1987, 119 in 1988, and 97 in 1989 (Table 1). We classified the fate of all except 19 nests. Of nests with known outcome, 37 of the 115 found during nest building eventually failed, 25 of the 106 found during incubation failed, and only 1 of the 135 found during the nestling period failed. Nesting success of species varied from 27% to 100% (Table 2).

Nesting success of excavators averaged across

　　　　　　　　　　　　　　　Li and Martin　　　　　　　　　　　　　

Table 2. Number of successful nests out of the total nests, number of days nests were observed, mean daily mortality (±SE), and nest success of cavity-nesting birds.

Species	Successful/total	Observation days	Daily mortality	Nest success
Excavators[a]				
Northern Flicker	34/34	680	0.000 ± 0.0015	100.0 (37)[b]
Red-naped Sapsucker	18/18	444	0.000 ± 0.0022	100.0 (38)
Williamson's Sapsucker	34/36	923	0.002 ± 0.0015	91.9 (42)
Hairy Woodpecker	7/8	142	0.007 ± 0.0070	75.5 (40)
Downy Woodpecker	3/3	73	0.000 ± 0.0136	100.0 (34)
Acorn Woodpecker	11/12	373	0.003 ± 0.0027	87.6 (44)
Red-breasted Nuthatch	8/11	259	0.012 ± 0.0066	68.8 (31)
Pygmy Nuthatch	16/18	384	0.005 ± 0.0037	83.1 (37)
Nonexcavators[c]				
Cordilleran Flycatcher	12/32	453	0.044 ± 0.0097	27.1 (29)
Mountain Chickadee	21/28	500	0.014 ± 0.0053	61.9 (34)
White-breasted Nuthatch	6/9	121	0.025 ± 0.0141	51.8 (26)
Brown Creeper	4/5	65	0.015 ± 0.0153	65.5 (28)
Western Bluebird	6/8	152	0.013 ± 0.0092	66.7 (31)
House Wren (all nests)	94/115	2,087	0.010 ± 0.0022	75.5 (28)
House Wren (in aspens)	79/95	1,824	0.009 ± 0.0022	77.6 (28)
House Wren (in maples)	14/19	251	0.020 ± 0.0088	56.8 (28)

[a] Red-breasted and Pygmy nuthatches sometimes use existing cavities.

[b] Numbers in parentheses are days of incubation and nestling periods. Nesting success is calculated based on these numbers.

[c] White-breasted Nuthatch sometimes excavate their own nests.

Table 3. Frequency (%) of tree condition types chosen for nest sites by cavity-nesting birds.

Bird species	Snag	Dead portion of live tree	Live tree	n
Excavators				
Northern Flicker	57	14	29	37
Red-naped Sapsucker	20	25	55	20
Williamson's Sapsucker	86	6	8	36
Hairy Woodpecker	50	25	25	8
Downy Woodpecker	67	0	33	3
Acorn Woodpecker	69	0	31	13
Red-breasted Nuthatch	86	7	7	14
Pygmy Nuthatch	78	11	11	18
Nonexcavators				
Cordilleran Flycatcher	37	4	30	27
Mountain Chickadee	59	7	34	29
White-breasted Nuthatch	70	10	20	10
Brown Creeper	100	0	0	5
House Wren	54	8	38	120
Western Bluebird	75	13	13	8
Average	60	9	29	348

[a] 30% of nests were in other sites, including broken-off trees, stumps, and roots of over-turned trees.

species was 88%, and nonexcavators was 58% (Table 2). Excavator species as a group had lower daily mortalities than nonexcavator species ($\chi^2 = 11.20$, df = 1, $P = 0.0008$). Exclusion of the species with the smallest sample sizes (Downy Woodpecker, *Picoides pubescens*, and Brown Creeper, *Certhia americana*) did not alter the pattern ($\chi^2 = 14.19$, df = 1, $P = 0.0002$). Exclusion of the nonexcavator species with the lowest nesting success (Cordilleran Flycatcher, *Empidonax difficilis*) also did not alter the difference between the two groups ($\chi^2 = 5.17$, df = 1, $P = 0.0230$). Excavator species did not differ among themselves in daily mortality ($\chi^2 = 5.94$, df = 7, $P = 0.55$), even if species with the smallest sample sizes (Hairy [*P. villosus*] and Downy woodpeckers) were excluded ($\chi^2 = 5.31$, df = 5, $P = 0.38$). Nonexcavator species differed marginally among themselves in daily mortality ($\chi^2 = 10.88$, df = 5, $P = 0.0531$), but more so when the species with the smallest sample size (Brown Creeper) was excluded ($\chi^2 = 10.88$, df = 4, $P = 0.0279$). The differences were caused by the low nesting success of the Cordilleran Flycatcher; exclusion of the Cordilleran Flycatcher yielded no difference among the remaining nonexcavator species ($\chi^2 = 1.628$, df = 4, $P = 0.80$).

TABLE 4. Percentage of nests found in various species of live trees and snags (>15 cm in DBH).

| Bird species | Tree species[a] | | | | |
	Aspen	Maple	Conifer	Other	n
Excavators					
Northern Flicker	97	0	3	0	37
Red-naped Sapsucker	100	0	0	0	20
Williamson's Sapsucker	97	0	3	0	36
Hairy Woodpecker	100	0	0	0	8
Downy Woodpecker	100	0	0	0	3
Acorn Woodpecker	100	0	0	0	13
Red-breasted Nuthatch	64	0	36	0	14
Pygmy Nuthatch	89	0	11	0	18
Nonexcavators					
Cordilleran Flycatcher	59	11	15	15	27
Mountain Chickadee	97	0	3	0	29
White-breasted Nuthatch	90	0	0	10	10
Brown Creeper	80	0	20	0	5
House Wren	83	16	1	0	120
Western Bluebird	100	0	0	0	8
Average use (U)[b]	88	6	5	1	
Availability (A)[c]	12	49	34	5	
Preference Index (U − A)/100	0.76	−0.43	−0.29	−0.04	

[a] Conifers include white fir, Douglas fir, ponderosa pine, and white pine. Other includes oak and locust.
[b] Average percentage that a tree species was used for nesting by all species.
[c] Availability was measured as the percentage of total trees that each species represented in 152 random plots.

Most nest losses were attributed to predation. We often observed squirrels and chipmunks entering birds' nesting cavities or being chased by parent birds, and we observed squirrels emerging from cavities with young or eggs. Two Williamson's Sapsucker (*Sphyrapicus thyroides*) nests were lost when nesting snags were blown down by strong wind.

Nest-site characteristics.—Habitat features were measured for 348 nests, 60% of which were in snags, 9% in dead portions of live trees, 2% in logs or stumps, and 29% in live trees (Table 3). All species except Red-naped Sapsuckers (*S. varius*) and Cordilleran Flycatchers nested primarily in snags. Several species had 30% or more of their nests in live trees, all of which were aspens, except 19 House Wren nests in maple. House Wrens nested mostly in cavities abandoned by excavators ($n = 100$), but some took advantage of natural cavities (e.g. cracks) in canyon maples ($n = 19$). Cordilleran Flycatchers placed 30% of their nests in other sites, such as broken-off trees, stumps, and in a depression among the roots of overturned trees.

Snags were used out of proportion to their availability ($\chi^2 = 202.5$, df = 3, $P < 0.005$; fewer than 10% of trees (>15 cm DBH) in random

plots ($n = 152$) were snags, but 60% of nests were in snags (Table 3). Of eight tree species used for nest sites (Table 4), aspens were used significantly more than their proportion in random plots ($\chi^2 = 481.3$, df = 1, $P < 0.005$). Aspens provided 88% of all nest sites, but constituted only 12% of all trees in random plots. Conifers and maples were underutilized relative to their availability ($\chi^2 = 23.9$, df = 1, $P < 0.005$, and $\chi^2 = 36.9$, df = 1, $P < 0.005$, respectively; Table 4). Thus, cavity-nesting species on these sites chose aspen out of proportion to abundance, and other tree types were used either in proportion to their abundance or underutilized (Table 4).

Habitat variables of nest sites differed from random plots for each species with sample sizes of >10 nests (Table 5). The overall percentages of nests and random plots correctly classified by discriminant function analyses (prior probabilities weighted by actual sample sizes) were greater than 70% for most species (Table 5). Northern Flickers (*Colaptes auratus*), Cordilleran Flycatchers, and House Wrens were least effectively discriminated from random sites, but each species still had habitat variables that differed from random plots (Table 5). Nest sites of most species had significantly more aspen snags and

TABLE 5. Results of discriminant function and univariate analyses that compare habitat characteristics of random plots (n = 152) with nesting sites of each species.[a] Levels of significance: * = $P < 0.05$; ** = $P < 0.01$. Sample sizes are in parentheses.

Variables	Bird species codes[b]										
	NF (37)	RS (20)	WS (36)	AW (13)	CF (27)	MC (29)	WN (10)	RN (14)	PN (18)	HR[c] (100)	HR[d] (19)
Aspens (>15 cm DBH)	0.367	0.000**	-0.876	-0.302	0.127	0.312	0.783	0.345	0.328	0.001**	0.350
Deciduous (8–15 cm)	-0.333	-0.000**	-0.011*	-0.778	0.405	-0.028*	-0.003**	0.781	-0.487	-0.067	0.551
Deciduous (>15 cm)	-0.330	-0.063	-0.011*	0.147	-0.844	-0.323	-0.431	-0.006**	-0.32*	-0.079	-0.134
Conifers (8–15 cm)	0.002**	-0.113	0.045*	0.682	-0.926	0.027*	0.015*	0.002**	0.611	0.407	0.382
Conifers (>15 cm)	0.006**	0.003**	0.000**	0.010**	0.013*	0.000**	0.000**	0.000**	0.001**	0.001**	0.063
Ground cover	-0.860	0.933	-0.578	-0.995	0.828	0.487	-0.543	-0.034*	-0.415	0.309	-0.407
Shrub cover (<3 m)	-0.731	-0.016*	0.495	0.020*	-0.021*	-0.064	-0.065	0.771	-0.795	-0.178	0.108
Aspen snags	0.000**	0.001**	0.000**	0.000**	0.271	0.000**	0.041*	0.010*	0.000**	0.000**	0.080
Conifer snags	0.004**	0.385	0.791	0.955	-0.785	0.088	0.068	0.000**	0.010*	0.070	0.930
Correctly classified by variables selected from stepwise analysis (%)	64.9	85.0	77.8	92.3	59.3	72.4	70.0	78.6	66.7	63.0	

[a] Values listed are significance levels between nest sites and random plots. Negative signs before values indicate values of nest sites are less than those of random plots.

[b] See Table 1 for bird species codes.

[c] House Wren nests in aspens.

[d] House Wren nests in maples vs. random maple sites (n = 19).

TABLE 6.   Nest height (m), nest-tree diameter breast height (cm), and body mass (g) of cavity-nesting birds.

Species	Nest height ($\bar{x} \pm$ SE)	Nest-tree DBH ($\bar{x} \pm$ SE)	Body mass[a]
Excavators			
Northern Flicker	16.3 ± 5.03	44.9 ± 8.45	130
Red-naped Sapsucker	13.3 ± 3.62	37.1 ± 5.83	45
Williamson's Sapsucker	12.4 ± 3.42	38.1 ± 8.93	43
Hairy Woodpecker	15.2 ± 6.44	37.1 ± 11.14	62
Downy Woodpecker	13.5 ± 4.77	35.7 ± 2.51	28
Acorn Woodpecker	17.4 ± 1.74	42.8 ± 6.10	67
Red-breasted Nuthatch	12.2 ± 4.35	48.4 ± 21.78	10
Pygmy Nuthatch	15.9 ± 4.78	45.3 ± 13.40	11.5
Nonexcavators			
Cordilleran Flycatcher	4.3 ± 4.24	35.0 ± 12.33	11
Mountain Chickadee	15.0 ± 5.08	39.8 ± 9.15	11.5
White-breasted Nuthatch	8.9 ± 4.31	35.0 ± 10.53	17.5
Brown Creeper	6.5 ± 3.04	30.8 ± 14.31	8
Western Bluebird	14.5 ± 2.16	38.8 ± 5.83	29.5
House Wren (all nests)	9.0 ± 4.33	33.6 ± 10.67	10.5
House Wren (in aspens)	9.7 ± 4.27	36.1 ± 8.05	
House Wren (in maples)	5.1 ± 2.05	18.1 ± 3.41	
Average	11.6 ± 5.60	37.8 ± 11.52	

[a] Body mass estimates from Martin (unpubl. data) and Terres (1980).

big conifers (>15 cm DBH) than random plots. The two species that did not choose sites with an abundance of aspen snags were the only ones that did not rely on aspen snags for nest sites (Cordilleran Flycatcher and House Wrens in maples, Table 5). House Wren nests in aspens were associated with more live aspens, big conifers, and aspen snags than random plots. Most species also exhibited a tendency to choose nest sites with reduced amounts of deciduous vegetation (Table 5). The consistent choice of these habitat features across species suggests that some habitat attributes may be generally important to all cavity-nesting species in their choice of nest sites.

Interspecific comparison.—Although species had commonalities in their nest sites as compared with random sites, species differed from each other in nest characteristics. Mean nest height of all cavity-nesting birds ranged from 4.3 m for Cordilleran Flycatchers to 17.4 m for Acorn Woodpeckers (Table 6). Nests of excavator species as a group were higher than nonexcavator species ($F = 120.6$, df = 1, $P < 0.0001$) even if rarer species (Downy Woodpecker and Brown Creeper) were excluded ($F = 114.9$, df = 1, $P < 0.0001$). However, nest heights of Mountain Chickadee (*Parus gambeli*) and Western Bluebird (*Sialia mexicana*) did not differ from excavator species ($P > 0.05$, Duncan's multiple range test).

Nonexcavator species differed among themselves in nest height ($F = 19.8$, df = 5, $P < 0.0001$), even if Mountain Chickadee and Western Bluebird were excluded ($F = 9.0$, df = 3, $P < 0.0001$). Excavator species also differed in nest height ($F = 4.1$, df = 7, $P = 0.0004$).

Mean nest-tree diameter (DBH) ranged from 18 cm for House Wrens in maples to 48 cm for Red-breasted Nuthatches (*Sitta canadensis*). Excavators as a group used nesting trees with larger DBH ($\bar{x} = 41.2$ cm, SE = 4.76) than nonexcavator species ($\bar{x} = 35.5$ cm, SE = 3.33, $F = 35.1$, df = 1, $P < 0.0001$). Diameter of nest trees did not differ among nonexcavator species ($F = 2.3$, df = 5, $P = 0.06$), but did differ among excavator species ($F = 3.26$, df = 7, $P = 0.005$). Finally, excavator species as a group had less foliage cover ($\bar{x} = 8.1\%$, SE = 18.5) near their nests than nonexcavator species ($\bar{x} = 18.5\%$, SE = 27.1, $F = 16.4$, df = 1, $P < 0.0001$), but foliage cover did not differ among species within either nest type ($F = 0.94$, df = 9, $P = 0.50$; Tables 7 and 8).

No species showed an orientation preference, nor did nonexcavators, failed or successful nests as groups. However, excavator species as a group exhibited a preference for eastern orientation ($\chi^2 = 18.20$, df = 7, $P < 0.025$), and they were significantly different from nonexcavator species in nest orientation ($\chi^2 = 24.16$, df = 7, $P < 0.005$).

TABLE 7. Means of habitat variables, univariate analyses, and discriminant function analysis among 6 main excavator species.[a] Levels of significance: * = $P < 0.05$, ** = $P < 0.01$. Sample sizes are in parentheses under species. Species codes are in Table 1.

| | Species | | | | | | Univariate analyses | | Step entered |
Variables	NF (37)	WS (36)	RS (20)	AW (13)	RN (14)	PN (18)	F	P	
Aspens (>15 cm)	2.54	2.33	4.75	1.31	2.93	2.72	2.46	0.036*	6
Deciduous (8–15 cm)	9.00	7.08	4.00	8.31	10.21	9.11	1.92	0.095	5
Deciduous (>15 cm)	6.05	5.08	5.30	9.08	3.50	4.44	1.97	0.087	
Conifers (8–15 cm)	3.84	3.17	1.00	2.39	4.57	2.67	2.61	0.028*	4
Conifers (>15 cm)	5.14	5.94	6.30	5.46	8.93	6.06	1.42	0.220	
Ground cover	0.53	0.50	0.54	0.53	0.37	0.47	0.87	0.506	
Shrub cover (<3 m)	0.30	0.32	0.21	0.43	0.31	0.29	2.35	0.044*	
Aspen snags	1.78	2.39	1.70	3.23	1.86	2.22	1.47	0.204	7
Conifer snags	0.87	0.50	0.55	0.46	1.29	0.94	2.20	0.058	3
Nest height (m)	16.3	12.4	13.3	17.4	12.2	15.9	5.35	0.000**	2
Nest tree DBH (cm)	44.9	38.1	37.1	42.8	48.4	45.3	2.80	0.020*	8
Nest concealment (%)	3.9	8.3	12.1	0.4	11.5	5.6	1.27	0.280	
Distance to conifer	8.1	5.1	6.1	7.5	4.2	6.3	6.04	0.000**	1
Correctly classified by 8 variables selected from stepwise analysis (%)	65.7	57.1	84.2	100	76.9	38.9			

[a] Primary cavity-nesting birds or excavators with large sample sizes.

The six main excavator species (Northern Flicker, Red-naped Sapsucker, Williamson's Sapsucker, Acorn Woodpecker [*Melanerpes formicivorous*], Red-breasted Nuthatch, and Pygmy Nuthatch [*Sitta pygmaea*] differed with respect to six nest-site variables (Table 7). They differed most in nest height and distance of nest site to the nearest conifer (Table 7). The Red-naped Sapsucker, Acorn Woodpecker, and Red-breasted Nuthatch differed from each other and all three other species based on their nest-site characteristics ($P < 0.05$, Mahalanobis distance), and they were classified with high accuracy.The other three excavator species did not differ from all species, and they were classified poorly (Table 7).

Nest sites of the four main nonexcavator species differed significantly in nest height, numbers of small deciduous trees, and nest-tree diameter (Table 8). Three of the four species (Cordilleran Flycatcher, Mountain Chickadee, and White-breasted Nuthatch [*Sitta carolinensis*]) were classified with reasonable accuracy (>70%) and differed from each other ($P < 0.05$, Mahalanobis distance). House Wrens were incorrectly classified more often than not (Table 8) and did not differ ($P > 0.05$, Mahalanobis distance) from the other species.

Cluster analysis produced four groups of spe-

cies at 0.12 semipartial R^2 values (Fig. 1). These groups roughly separated excavator from nonexcavator species. The first group included two nonexcavator species (Brown Creeper and House Wren in maples). The second group included three nonexcavator species (Cordilleran Flycatcher, White-breasted Nuthatch, and House Wren in aspens). The third group included three excavator species (Williamson's Sapsucker, Red-breasted Nuthatch, and Downy Woodpecker) and one nonexcavator species (Western Bluebird). The final group included five excavator species (Northern Flicker, Red-naped Sapsucker, Hairy Woodpecker, Acorn Woodpecker, and Pygmy Nuthatch) and one nonexcavator species (Mountain Chickadee).

Nest site and nesting success. —We compared failed nests to successful nests for all species combined except House Wrens, which were excluded because their large sample size would swamp the remaining sample. The analysis indicated that failed nests were lower in height (9.9 m vs. 13.5 m, $P = 0.0006$), had more foliage cover (23.6% vs. 9.3%, $P = 0.0006$), and more large conifers (2.7 vs. 2.3 trees, $P = 0.021$) than successful nests.

Sample sizes for Cordilleran Flycatcher, Mountain Chickadee, and House Wren were sufficient for individual species analyses of suc-

TABLE 8. Means of habitat variables, univariate analyses, and discriminant analysis among 4 main nonexcavator species.[a] Levels of significance: * = $P < 0.05$, ** = $P < 0.01$. Sample sizes are in parentheses under species. Species codes are in Table 1.

Variables	Species				Univariate analyses		Step entered
	CF (27)	MC (29)	WN (10)	HR (120)	F	P	
Aspens (>15 cm)	2.63	2.66	2.10	2.95	0.23	0.878	
Deciduous (8–15 cm)	10.59	7.07	3.80	8.34	3.73	0.012*	2
Deciduous (>15 cm)	7.19	6.17	5.70	6.05	0.15	0.927	
Conifers (8–15 cm)	2.00	3.48	3.90	2.37	2.19	0.090	
Conifers (>15 cm)	5.41	6.28	7.90	4.72	2.28	0.081	
Ground cover	0.42	0.57	0.49	0.56	2.41	0.068	4
Shrub cover (<3 m)	0.30	0.23	0.20	0.30	1.89	0.133	
Aspen snags	1.22	2.07	1.50	1.79	1.91	0.129	
Nest height (m)	4.3	15.0	8.9	9.0	27.35	0.000**	1
Nest tree DBH (cm)	35.0	39.8	35.0	33.6	2.65	0.050*	3
Nest concealment (%)	20.0	16.0	14.0	19.0	0.22	0.883	
Correctly classified by 4 variables selected from stepwise analysis (%)	81.5	75.9	80.0	45.8			

[a] Nonexcavator species with large sample sizes.

cessful versus failed nests. Failed and successful nests of Cordilleran Flycatchers did not differ in any habitat characteristics based on univariate analyses. However, multivariate analyses indicated they were significantly different ($P = 0.0016$, Mahalanobis distance), and they were classified with high accuracy based on stepwise discriminant function analysis (Table 9). In contrast, both univariate and multivariate analyses ($P = 0.006$, Mahalanobis distance) indicated differences between failed and successful nests of Mountain Chickadees; failed nests had more foliage cover and were closer to conifers than successful nests (Table 10). Failed Mountain Chickadee nests also had marginally more large conifers and deciduous trees nearby (Table 10). We analyzed House Wren nests only in aspen because nests in maples were very different (Fig. 1, Table 5), and sample size for nests in maples was too small for analysis. Failed nests of House Wrens in aspens were associated with more large deciduous trees and greater nest cover than successful nests, and discriminant analysis ($P = 0.0019$, Mahalanobis distance) correctly classified approximately 70% of the nests (Table 11).

We tested the relationship between nesting success and means of nest height, nest concealment, body mass, and the distance to conifer tree for the 14 cavity-nesting species. Nesting success of the 14 species was significantly correlated with nest height, nest concealment, and body mass of each species, but not with distance

to conifer tree (Table 12). However, these variables were intercorrelated (Table 12). Partial correlation analysis indicated that nest height was significantly correlated with nesting success when body mass was controlled ($r_p = 0.522$, $P = 0.034$), but only marginally correlated when nest concealment was controlled ($r_p = 0.422$, $P = 0.075$). The latter result reflects the tight cor-
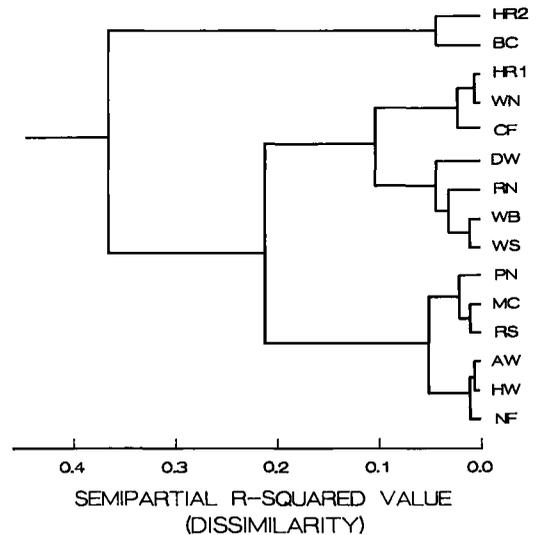

Fig. 1. Cluster analysis of cavity-nesting species based on Euclidean distances between mean values of habitat variables. See Table 1 for species codes.

TABLE 9. Univariate and discriminant analyses that compare habitat and nest characteristics of successful nests ($n = 11$) with failed nests ($n = 13$) of Cordilleran Flycatcher.

Variables	Successful ($\bar{x}$)	Failed ($\bar{x}$)	Univariate analyses		Step entered
			F	P	
Aspens (>15 cm)	3.18	2.31	0.45	0.510	
Deciduous (8–15 cm)	12.18	9.23	1.32	0.263	2
Deciduous (>15 cm)	8.73	5.85	1.86	0.187	4
Conifers (8–15 cm)	2.82	1.69	3.11	0.092	1
Conifers (>15 cm)	5.18	6.23	0.25	0.624	
Ground cover	0.44	0.37	0.58	0.455	3
Shrub cover (<3 m)	0.30	0.31	0.00	0.957	5
Aspen snags	1.00	1.54	0.17	0.685	
Nest height (m)	4.4	4.3	0.01	0.928	
Nest tree DBH (cm)	31.5	36.4	1.02	0.323	
Nest concealment (%)	22.7	17.7	0.33	0.570	
Correctly classified by the 5 variables selected from stepwise analysis	92.3%	81.8%			

relation between nest height and nest concealment ($r = -0.801$, $P < 0.0001$). Body mass ($r_p = 0.317$, $P = 0.146$) and nest concealment ($r_p = -0.167$, $P = 0.292$) were not correlated nesting success when nesting height was controlled, which indicates the primary importance of nest height to nesting success in interspecific comparisons.

DISCUSSION

Cavity-nesting species on our study sites consistently chose nest patches with more aspen snags, live aspens, and large conifers than there

were on random plots. The tendency to choose patches with more aspens may reflect choice of patches with more potential nest sites, as aspens provided 88% of all nest sites. More potential nest sites near a nest may reduce predator efficiency because predators should be forced to search more sites to find nests (Martin 1988c, Martin and Roper 1988). However, comparisons of successful with failed nests did not show that successful nests were associated with more aspen snags. Nonetheless, choice of patches with abundant aspen snags reflected choice of patches with an abundance of sites that were used for nesting but not foraging. We rarely found

TABLE 10. Univariate and discriminant analyses that compare habitat and nest characteristics of successful nests ($n = 21$) with failed nests ($n = 7$) of Mountain Chickadee. Levels of significance: * = $P < 0.05$, ** = $P < 0.01$.

Variables	Successful ($\bar{x}$)	Failed ($\bar{x}$)	Univariate analyses		Step entered
			F	P	
Aspens (>15 cm)	2.38	3.00	0.32	0.575	
Deciduous (8–15 cm)	6.62	9.14	0.68	0.416	
Deciduous (>15 cm)	6.95	3.00	3.36	0.078	2
Conifers (8–15 cm)	3.81	2.71	0.54	0.468	
Conifers (>15 cm)	5.48	8.71	3.30	0.081	
Ground cover	0.61	0.42	2.35	0.137	
Shrub cover (<3 m)	0.25	0.19	1.13	0.298	
Aspen snags	1.95	2.14	0.13	0.722	
Nest height (m)	14.3	15.6	0.39	0.538	
Nest tree DBH (cm)	39.4	40.1	0.04	0.854	
Nest concealment (%)	8.6	40.7	8.12	0.009**	1
Distance to conifers (m)	6.4	3.3	4.37	0.047*	
Correctly classified by the 2 variables selected from stepwise analysis (%)	81.0	71.4			

TABLE 11. Univariate and discriminant analyses that compare habitat and nest characteristics of successful House Wren nests ($n = 79$) with failed nests ($n = 16$) on aspens. Levels of significance: * = $P < 0.05$, ** = $P < 0.01$.

Variables	Nests		Univariate analyses		Step entered
	Successful ($\bar{x}$)	Failed ($\bar{x}$)	F	P	
Aspens (>15 cm)	3.60	2.56	2.26	0.136	
Deciduous (8–15 cm)	8.14	7.94	0.45	0.506	
Deciduous (>15 cm)	5.24	9.25	10.47	0.002**	1
Conifers (8–15 cm)	2.58	2.63	0.02	0.878	
Conifers (>15 cm)	5.43	3.75	1.53	0.219	
Ground cover	0.55	0.68	2.58	0.112	3
Shrub cover (<3 m)	0.26	0.31	1.83	0.180	
Aspen snags	2.03	2.19	0.27	0.602	
Nest height (m)	9.4	10.4	0.55	0.459	
Nest tree DBH (cm)	35.6	36.8	0.28	0.602	
Nest concealment (%)	14.4	29.0	3.72	0.057	2
Distance to conifers (m)	6.4	6.3	0.04	0.837	
Correctly classified by the 3 variables selected from stepwise analysis (%)	78.5	62.5			

evidence for foraging on aspens on the sites (pers. obs.).

The preference for patches with more conifers may reflect a choice of patches with abundant foraging substrates. Conifers were used for foraging by most cavity-nesting species (pers. obs., also see Mannan et al. 1980, Raphael and White 1984, Swallow et al. 1986). In other Arizona pine forests cavity nesters probably do not compete for limited food (Brawn et al. 1987). However, food may still limit reproductive performance and, secondarily, influence patch choices (Martin 1987). Yet, failed nests had more large conifers nearby than successful nests. Failure was usually attributable to predation. The presence of large conifers might attract predators and increase the risk of discovery. Red squirrels are primary nest predators on these

sites (Martin 1988c, pers. obs.), and they focus many of their activities in large conifers (Uphoff 1990). Thus, choice of patches with an abundance of conifers may increase food availability for reproduction, but may also increase the risk of nest predation.

Nest patches generally had fewer deciduous trees than random plots for most bird species (Table 5). More deciduous trees at nest patches can increase foliage cover and nest concealment. Failed nests in our study, particularly those of Mountain Chickadees and House Wrens, were more concealed by foliage than successful nests. A similar result for House Wrens was reported by Belles-Isles and Picman (1986) and Finch (1989). Greater foliage cover around cavity nests may increase nest predation because parent birds may have difficulty de-

TABLE 12. Correlation coefficients between nesting success and nest height (NH), nest concealment (NC), distance to nearest conifer (DC), and body mass (BM) of each species.[a]

Variable	NH	NC	DC	BM
Nesting success	0.694	−0.627	0.158	0.581
	0.004	0.012	0.573	0.023
Nest height		−0.801	0.192	0.567
		0.000	0.491	0.028
Nest concealment			−0.026	−0.524
			0.928	0.045
Distance to nearest conifer				0.556
				0.031

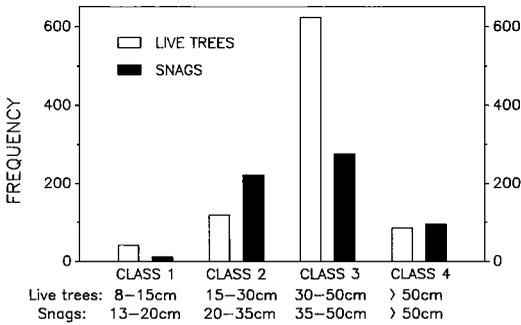[a] Values below correlation coefficients are significance levels.

Fig. 2. Abundance of aspens in random plots by DBH classes.

tecting and deflecting approaching predators (Nilsson 1984, Belles-Isles and Picman 1986, Finch 1989). Similarly, increased rates of nest failure for lower nests may occur because predators are able to detect and approach such nests without being identified and attacked by parents (Nilsson 1984). Low nests also are usually more concealed than higher nests. Perhaps birds compete for higher nests as part of their reproductive success.

On the other hand, concealment of nests is not always detrimental. Open-nesting species with more concealed nests are more successful (reviewed in Martin 1991a). Moreover, Cordilleran Flycatcher had the lowest nesting success (27%) probably because it had the most exposed nests among all species. Most of their nests were located very low on the edge of tree holes, edge of logs or stumps, or on other open ledge-type situations. Yet this species was atypical of the remaining cavity-nesters, and the general analysis indicated that greater foliage concealment for most cavity-nesters was usually associated with greater probability of nest failure.

Excavator species had significantly higher nesting success than nonexcavator species (Table 2). This occurred in part because nonexcavators nest in older cavities. Predators often prey more extensively on old cavities (Sonerud 1985, 1989). Mountain Chickadees are similar in body size and nest height to Pygmy Nuthatches (see Table 6), but Chickadees depend on old holes while Pygmy Nuthatches excavate new ones. Mountain Chickadees have lower nesting success (Table 2). However, the difference between excavator and nonexcavator species in nesting success cannot be attributed to nest age alone.

Nonexcavator species also nested at generally lower heights than excavator species, and lower nests are subject to greater rates of failure. For example, the House Wren nested at lower heights in maple than aspen (Table 6), and nesting success was lower in maple than in aspen (Table 2). Nonexcavator species are generally smaller than excavator species. This smaller size may reduce ability to compete for higher nests and produce the correlation between body size and nest height (see Table 12). Small body size may directly affect vulnerability to nest predation because smaller birds may be less effective at deflecting larger predators (also see Martin 1991b). Presumably, lower nests, smaller body size, and older nest age may all interact to cause greater nest failure for nonexcavator as compared with excavator species.

Competition for limited nest sites may force use of suboptimal sites. House Wrens were the most abundant species (Martin upubl. data), and competition for nest sites may be more stringent than for other species. We observed several cases of fighting and defense of nest cavities by House Wrens from conspecifics and other species, as have others (e.g. see Brawn and Balda 1988). The lack of difference of habitat variables between nest sites and random plots for House Wrens in maples may imply that maples were not a preferred nest site and were used when preferred sites were unavailable. This interpretation was supported by the relatively low frequency (15%) of nests in maples and by the nesting success being lower in maples than in aspens (Table 2).

Cavity-nesting species typically differ in habitat characteristics of the chosen patches. Different species may select different nesting habitats to avoid interspecific competition for food (see Cody 1985), or reduce density-dependent responses of predators (see Martin 1988a, c). These responses may favor differences in habitat use among related species and could form the basis of speciation. A cluster analysis showed the two sapsucker species differed in habitat characteristics of nest sites, and the three nuthatch species also differed from each other (Fig. 1). Species that shared similar nesting habitats generally exploited different resources and belonged to different foraging guilds.

Aspens are the preferred nest sites, and management in this forest is important to cavity-nesting birds. Large trees are abundant in this

aspen population, but young trees are scarce (Fig. 2, based on the counts of aspens in random plots). Dead trees accounted for approximately 40% of the total population. Aspen generally moves in after wood-harvesting or fires. The large aspens in this area perhaps grew after extensive harvests of conifers many years ago. Now, as young conifers grow, aspens gradually decline. Clearly, the aspen population is declining (Fig. 2). Continued succession that results in continued loss of aspens may escalate competition for nest sites for cavity-nesting birds. Populations of cavity-nesting birds might decrease unless alternative nest trees (e.g. conifers) are used, but conifer snags are rare in this forest because most large conifers are harvested before they die. The general importance of the abundance of nest sites provided by aspen is indicated by the extremely diverse (14 species) assemblage of cavity nesters that existed on these sites where conifer snags were rare.

LITERATURE CITED

BELLES-ISLES, J., & J. PICMAN. 1986. Nesting losses and nest site preferences in House Wrens. Condor 88: 483–486.

BRAWN, J. D., & R. P. BALDA. 1988. Population biology of cavity nesters in Northern Arizona: Do nest sites limit breeding densities? Condor 90: 61–71.

———, W. J. BOECKLEN, & R. P. BALDA. 1987. Investigations of density interactions among breeding birds in ponderosa pine forests: correlative and experimental evidence. Oecologia 72: 348–357.

BRUSH, T., B. W. ANDERSON, & R. D. OHMART. 1983. Habitat selection related to resource availability among cavity-nesting birds. Pp. 88–98 *in* Snag habitat management: proceedings of the symposium. U.S. Dep. Agric. For. Serv. Tech. Rep. RM-99.

CLINE, A., B. BERG, & H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44: 773–786.

CODY, M. L. 1985. An introduction to habitat selection in birds. Pp. 3–56 *in* Habitat selection in birds (M. L. Cody, Ed.). Orlando, Florida, Academic Press.

CONNER, R. N. 1975. Orientation of entrances to woodpecker nest-cavities. Auk 92: 371–374.

DAVIS, J. W., G. A. GOODWIN, & R. A. OCKENFELS (Eds.). 1983. Snag habitat management: proceedings of the symposium. U.S. Dep. Agric. For. Serv. Tech. Rep. RM-99.

FINCH, D. M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in House Wrens. Condor 91: 848–859.

GUTZWILLER, K. J., & S. H. ANDERSON. 1987. Multiscale associates between cavity-nesting birds and features of Wyoming streamside woodlands. Condor 89: 537–548.

HENSLER, G. L., & J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93: 42–53.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

MANNAN, R. W., E. C. MESLOW, & H. M. WIGHT. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44: 787–797.

MARTIN, T. E. 1987. Food as a limit on breeding birds: a life history perspective. Annu. Rev. Ecol. Syst. 18: 453–487.

———. 1988a. Processes organizing open-nesting bird assemblages: competition or nest predation? Evol. Ecol. 2: 37–50.

———. 1988b. Habitat and area effects on organization of forest bird assemblages: Is nest predation an important underlying influence? Ecology 69: 74–84.

———. 1988c. On the advantages of being different: nest predation and coexistence of birds species. Proc. Natl. Acad. Sci. USA. 85: 2196–2199.

———. 1991a. Breeding productivity considerations: What are the appropriate habitat features for management? *In* Ecology and conservation of Neotropical migrants (J. Hagan and D. W. Johnston, Eds.). Washington, D.C., Smithson. Inst. Press. In press.

———. 1991b. Interaction of nest predation and food limitation in reproductive strategies. Curr. Ornithol. 9. In press.

———, & J. J. ROPER. 1988. Nest predation and nest site selection of a western population of the Hermit Thrush. Condor 90: 51–57.

MARZLUFF, J. M., & L. J. LYON. 1983. Snags as indicators of habitat suitability for open nesting birds. Pp. 140–146 *in* Snag habitat management: proceedings of the symposium. U.S. Dep. Agric. For. Serv. Tech. Rep. RM-99.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73: 255–261.

———. 1975. Suggestions for calculating nest success. Wilson Bull. 87: 456–466.

MUNRO, H., & R. C. ROUNDS. 1985. Selection of artificial nest sites by five sympatric passerines. J. Wildl. Manage. 49: 264–476.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74: 305–321.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15: 165–175.

PETERSON, B., & G. GAUTHIER. 1985. Nest site use by cavity-nesting birds of the Caribou Parkland, British Columbia. Wilson Bull. 97: 319–331.

RAPHAEL, M. G., & M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. No. 86.

RELLER, A. W. 1972. Aspects of behavioral ecology of Red-headed and Red-bellied woodpeckers. Am. Midl. Nat. 88: 270–290.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9: 1–48.

RUNDE, D. E., & D. E. CAPEN. 1987. Characteristics of northern hardwood trees used by cavity-nesting birds. J. Wildl. Manage. 5: 217–223.

SAS. 1985. SAS user's guide. Cary, North Carolina, SAS Inst.

SAUER, J. R., & B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. J. Wildl. Manage. 53: 137–142.

SCOTT, T. V., K. E. EVANS, D. R. PATTON, & C. P. STONE. 1977. Cavity-nesting birds of North American forests. Washington, D.C., U.S. Dep. Agric. For. Serv. Agric. Handb. 511.

SCOTT, V. E. 1978. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. J. For. 76: 26–28.

———. 1979. Bird response to snag removal in ponderosa pine. J. For. 77: 26–28.

SEDGWICK, J. A., & F. L. KNOPF. 1990. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. J. Wildl. Manage. 54: 112–124.

SONERUD, G. A. 1985. Nest hole shift in Tengmalm's Owl, *Aegolius funereus*, as defence against nest predation involving long-term memory in the predator. J. Anim. Ecol. 54: 179–192.

———. 1989. Reduced predation by pine martens on nests of Tengmalm's Owl in relocated boxes. Anim. Behav. 37: 332–334.

STAUFFER, D. F., & L. B. BEST. 1982. Nest site selection by cavity-nesting birds of riparian habitats in Iowa. Wilson Bull. 94: 329–337.

SWALLOW, S. K., R. J. GUTIERREZ, & R. A. HOWARD. 1986. Primary cavity-site selection by birds. J. Wildl. Manage. 50: 576–583.

TERRES, J. K. 1980. The Audubon Society encyclopedia of North American birds. New York, Alfred A. Knopf, Inc.

UPHOFF, K. C. 1990. Habitat use and reproductive ecology of Red Squirrels (*Tamiasciurus hudsonicus*) in central Arizona. M.S. thesis, Arizona State Univ.