HABITAT SUITABILITY FOR WILLIAMSON'S SAPSUCKERS IN MIXED-CONIFER FORESTS

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Abstract: Williamson's sapsuckers (Sphyrapicus *thyrotdeus*) have narrow habitat requirements and are sensitive indicators of change in intensively managed forest habitats of western North America. Thus, we studied habitat suitability for Williamson's sapsuckers at 99 4-ha sites (33 nest sites, 66 non-use sites) in **mixed**-conifer forests in Arizona during 1991. Nesting success of sapsuckers was high in this habitat (93.2% nest success, **0.0014** daily mortality, n = 724 nest days), and they preferred to nest in tall (P < 0.05) aspen snags (P < 0.001) near the bottom (P = 0.012) of snow-melt drainages with 0–20% of the canopies dominated by aspen. Sapsucker nest sites had particularly large (P < 0.05) live aspen and aspen snags in the surrounding area. Nest sites also had high (P < 0.05) snag densities (a = 7.65 snags/ha) in the surrounding area, and these snag densities exceeded those commonly used in forest management plans. Effective snag management should concentrate snags in groups within low-lying areas and conserve large-sized snags. A Habitat Suitability Index (HSI) correctly predicted that Williamson's sapsuckers should generally prefer drainages over ridgetops, but the model could not distinguish between use and non-use sites within drainages. Future **HSI** models for Williamson's sapsucker should continue to stresssnag density, but should consider aspen snag density separately from density of other snags, incorporate height and diameter of aspen snags, and use a more liberal definition of aspens contributing to overstory canopy cover.

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Forest managers are faced with trying to maintain viable populations of vertebrates while simultaneously managing for other resource needs such as timber production. This delicate balancing act depends upon knowing the effects of land management practices on habitat suitability for wildlife. The first step in attaining this knowledge is to identify habitat features that influence habitat suitability. Moreover, identification of habitat features that directly affect reproduction and survival is the most effective means of indexing habitat suitability because maintenance of viable populations depends on sustaining these fitness components (Martin 1992).

Cavity-nesting birds are a particularly appropriate group of species for examining effects of land management on habitat suitability because they are often affected by land management practices (Gysel 1961, Haapanen 1965, Hunter 1990). For instance, snags are less abundant in managed than unmanaged forests (Cline et al. 1980), and availability of snags commonly limits populations of cavity-nesting birds by **lim**-

iting nesting opportunities (for review, see Li and Martin [1991], Martin and Li [1992]). In response, explicit policies for snag conservation have been implemented for managed stands (Hunter 1990). Yet, management for presence of snags is not sufficient; size, species, and age of snags, plus distribution of nest trees and vegetation in surrounding patches can affect presence and even reproductive success of birds (Flack 1976, Raphael and White 1984, Sedgwick and Knopf 1990, Li and Martin 1991). Key habitat features that influence habitat suitability, particularly with regard to reproduction or survival, need to be identified for individual species.

Williamson's sapsucker is the least numerous and most ecologically and genetically specialized species in its genus (Crockett and Hadow 1975, Johnson and Zink 1983). They are most common in middle-elevation forests of ponderosa pine (*Pinus* ponderosa) and Douglas-fir (Pseudotsuga menziesii), 2 forest types that are managed intensively for timber extraction in western North America (Thomas et al. 1979b). Within these intensively managed forests, Williamson's sapsuckers have narrow habitat requirements and limited versatility, making them sensitive indicators of environmental changes (Thomas et al. 1979b). Consequently, a Habitat

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Suitability Index (HSI) model was developed for use in evaluating management plans (Sousa 1983).

Williamson's sapsuckers excavate nests most commonly in quaking aspens (Populus tremuloides) within coniferous forests (Crockett and Hadow 1975, Smith 1982, Sousa 1983), and habitat requirements are considered more restrictive for reproduction than feeding (Thomas et al. 1979b). Yet, quantitative descriptions of habitat preferences are lacking. Previous studies have assumed strict nest site preferences (Rasmussen 1941, Hubbard 1965, Tatschl 1967, Crockett and Hadow 1975) but results probably reflected nest site availability within different forest stands (Erskine and McLaren 1972). Sites used for nesting need to be compared with non-use sites within the same general type of vegetation to determine key habitat features associated with sites chosen for reproduction.

Herein, we present data on nesting habitat and breeding success for Williamson's sapsuckers from nest sites and non-use sites. We examined nest site preferences by comparing habitat at nest sites to non-use sites. In addition, we compared nest placement characteristics to those from previous studies. We also evaluated the efficacy of the HSI model (Sousa 1983) for predicting nesting use of the sites that we sampled in ponderosa **pine/Douglas-fir** forests in central Arizona.

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STUDY AREA

We conducted our research on the Mogollon Rim of central Arizona (about 2,300-m elevation). Study sites were snow-melt drainages and intervening ridges. The drainages had a mixed overstory of ponderosa pine, white fir (Abies concolor), Douglas-fir, southwestern white pine (*Pinus* strobiformis), quaking aspen, and Gambel oak (Quercus gambelii). Young plants of these canopy trees, plus bigtooth maple (Acer grandidentatum) and New Mexico locust (Robinia neomexicana), dominated the understory woody species (see Martin 1988*a* for detailed description). The drainages differed from the surrounding ridges, which primarily supported a ponderosa pine overstory, a Gambel oak subcanopy, and had little understory vegetation.

METHODS

We searched 14 drainages and ridges for nests from mid-May to mid-July in 1991. Nests were located by observing parents building or entering nests, and then confirmed by observing adults entering later to incubate eggs or feed young, or by directly observing young in the nest. Nests were checked every 3-4 days to monitor success (Li and Martin 1991). We considered nests successful if ≥ 1 young fledged.

We recorded nest tree species, nest height, tree height, nest hole orientation, and age of nest hole (new or old excavation) at 33 nest sites during this study and included similar data from 33 nest sites examined on these study areas in previous years (Li and Martin 1991). In 1991, we also measured a number of habitat features in the 4-ha patch surrounding the nest tree and in 2 distinct non-use sites of the same size that were located adjacent to each nest site. One nonuse site was located within the same drainage as the nest site, alternating up or down the drainage, and the other non-use site was located perpendicular to the nest drainage, generally falling on the upper slope or nearby ridgetop. This allowed us to determine whether Williamson's sapsuckers chose territories based on drainage characteristics and whether they chose nest sites within preferred drainages based on patch characteristics. We chose 4-ha plots to sample habitat features based on previously published estimates of territory size for Williamson's sapsuckers (Thomas et al. 1979a, Sousa 1983). Subsequently, additional habitat features were measured in 33 nest sites and 66 non-use sites in 1991. We measured density and size of aspen trees and snags in each of these 4-ha sites.

The HSI model for the Williamson's sapsucker incorporates **4** habitat variables **by** which it evaluates the suitability of reproductive habitat for the inland subspecies (S. t. nataliae) (Am. Ornithol. Union **1957**). These variables are percent canopy cover, percent of canopy dominated by aspen, dbh of "overstory" aspen trees, and density of "suitable" snags in the 4-ha patch surrounding the nest (Sousa 1983). We measured these 4 variables in the 4-ha sites from 1991 to test the HSI model. We used spherical crown densiometers (Lemmon 1956) to estimate percent canopy cover at 30 evenly spaced points throughout a 4-ha grid surrounding each nest and non-use site. Percent canopy dominated by aspen was determined by the proportion of the 30 points where aspen was the dominant canopy species. We established 3 evenly spaced, 25-× 200-m transects in each 4-ha grid accounting for 37.5% (1.5 ha) of the total area of each grid. At nest sites, the actual nest tree determined the center of the middle transect. The center of the non-use sites were determined by pacing 230 m from the nest tree. leaving a 30-m buffer between the 200-×200-m nest sites and adjacent non-use sites. The dbh and height of all snags and live aspen trees ≥ 18 cm dbh were noted in each transect. We considered trees ≥ 18 cm dbh as available nest trees based on previous studies of Williamson's sapsucker nest site selection (Crockett and Hadow 1975).

In addition to average dbh and average height of live and dead aspen trees, we also estimated the number of "suitable" snags per ha and the average dbh of "overstory" aspen trees in both use and non-use sites. "Suitable" snags were defined by the HSI model as dead ponderosa pine trees \geq 45.7 cm dbh and soft snags of all other trees \geq 30.5 cm dbh that are in advanced stages of decay and deterioration (Sousa 1983). "Overstory" aspen trees were defined by the model as those aspen that are $\geq 80\%$ of the height of the tallest tree in the stand (Sousa 1983). To examine the distribution of potential nest sites within preferred nesting habitat, we estimated aspen snag densities within the 0.8-ha block of habitat surrounding the nest tree and within the 3.2 ha on the perimeter of the nest plots. We compared snag densities between these 2 zones within nest plots with paired t-tests (SAS Inst. Inc. 1985). We visited sites daily to search for new nests and were very confident that non-use sites did not contain additional nesting pairs of sapsuckers.

We compared differences in use of nest trees versus available trees with a Chi-square goodness-of-fit test (Zar 1984). Pearson product-moment partial correlations (r) and associated significance probabilities (SAS Inst. Inc. 1985) were calculated to examine relationships among habitat variables and between habitat variables and HSI ratings. We tested all variables for normality by examining Shapiro-Wilks' W-statistic and normal probability plots (SAS Inst. Inc. 1985). Tree height, percent canopy cover, number of "suitable" snags, and aspen snag densities within nest plots were normally distributed (P > 0.01, Shapiro-Wilks' test). Distributions of all other habitat variables were non-normal (P < 0.01, Shapiro-Wilks' test), but unimodal. We used univariate analysis of variance (ANOVA) with Bonferroni multiple comparisons (SAS Inst. Inc. 1985) to examine differences in habitat variables among nest and both types of non-use plots. We used paired t-tests (SAS Inst. Inc. 1985) to examine differences in snag densities within nest plots. Although some of our habitat variables were not normally distributed, we chose to use parametric statistics because these statistics are robust under violations of normality (Boneau 1960, Donaldson 1968, Harris 1985).

RESULTS

Williamson's sapsuckers usually excavated new cavities for nesting (79%, n = 28) rather than using old holes. However, nests showed no orientation preference ($\chi^2 = 2.42, 3 df, P = 0.50$). Of 66 nests, most (54) were in aspen snags, some (11) were in live aspen trees, and one was in an unidentified snag. Densities of live aspen $(9.2 \pm$ 7.4 trees/ha) were greater than aspen snags (3.6) \pm 2.2 snags/ha) or other snags (4.1 \pm 2.8/ha) on the 99 4-ha sites sampled. Thus, aspen snags were used more ($\chi^2 = 99.49$, 1 df, P < 0.001) than expected based on their availability. No nests were found in conifer snags despite similar availability. Percent of canopy dominated by aspen ranged from 0–20% ($\bar{x} = 7 \pm 6\%$) within Williamson's sapsucker nest plots.

Nest height averaged $13.1 \pm 5.3 \text{ m}$ (range = 3-26 m, n = 31) and was correlated with nest tree height (r = 0.69, n = 23, P < 0.0003), but not nest tree dbh (r = 0.19, n = 23, P = 0.3841). Live aspens used for nesting $(20.7 \pm 3.5 \text{ m})$ range = 16-26 m, n = 6) were similar (P > 0.05) in height to available live aspen trees (21.9 \pm 3.0 m, range = 6.1-32.0 m, n = 530) within nest plots. In contrast, aspen snags used for nesting (24.9 + 4.8 m, range = 15-33.5, n = 24)were taller (P < 0.05) than available aspen snags $(19.7 \pm 5.7 \text{ m}, \text{ range} = 3.4-29 \text{ m}, \text{ n} = 207)$ within nest plots. Diameter (dbh)of live aspens used for nesting $(36.2 \pm 7.4 \text{ cm}, \text{ range} = 30 -$ 50.8 cm, n = 6) did not differ (P > 0.05) from dbh of available live aspen trees $(37.2 \pm 8.2 \text{ cm})$ range = 19-70 cm, n = 532) within nest plots. Similarly, dbh of aspen snags used for nesting $(38.1 \pm 10.6 \text{ cm}, \text{ range} = 25-63.5 \text{ cm}, \text{ n} = 23)$ did not differ (P > 0.05) from dbh of available aspen snags $(37.2 \pm 8.0 \text{ cm}, \text{ range} = 20.3-65)$ cm, n = 207) within nest plots. Thus, live aspen trees used for nesting were generally similar in

Characteristic	Nests		Non-use ^a		Non-use ^b	
	Ī	SD	Ĩ	SD	Ĩ	SD
HSI rating	0.934	0.12	0.790	0.29	0.650	0.34*
% canopy cover	0.559	0.11	0.582	0.13	0.531	0.13
% aspen cover	0.070	0.06	0.082	0.08	0.035	0.07
Dbh of aspen (cm) ^c	8.05	9.77	5.79	7.73	3.13	7.88
Total snag density (No./ha)	7.65	3.94*	5.31	3.22*	2.96	2.19*
Live aspen density (No./ha)	9.17	7.37	8.97	10.18	3.68	5.23*
Aspen snag density (No./ha)	3.56	2.18	2.42	2.85	0.46	1.05*
Total aspen density (No./ha)	12.73	8.91	11.39	12.45	4.14	6.00*

Table 1. Habitat characteristics within 4-ha nest plots (n = 33) and non-use plots (n = 33 each) for Williamson's sapsucker, central Arizona, 1991.

^a Within drainage of nest plot.

^b Outside drainage of nest plot.

^c Aspen trees 280% of the height of the tallest tree in the stand.

* Differs (P < 0.05) from the other 2 groups (ANOVA, Bonferroni comparisons).

size to other live aspens available in nest plots, but aspen snags used for nesting were taller than available aspen snags within the nest plots.

Of 31 nests, most ($\chi^2 = 13.054$, 4 df, P = 0.012) nest trees were at the bottom of a drainage (35%), on the lower third of a slope (29%), or on the middle third of a slope (26%). Only a small proportion were found on the upper third of a slope (10%) or on a ridgetop (0%). Nest plots had more (P < 0.05) snags than non-use plots inside or outside of drainages and more (P <0.05) live aspen trees and aspen snags than nonuse plots outside the nest drainage (Table 1). Aspen snags were not randomly distributed. The 0.8-ha block of habitat immediately surrounding the nest trees had higher (t = 5.603, P < 0.0001) aspen snag densities $(8.89 \pm 5.35 \text{ snags}/$ ha, n = 31) than the 3.2 ha on the perimeter of the nest plots $(3.19 \pm 2.26 \text{ snags/ha}, n = 31)$.

Live aspen trees ($\bar{x} = 21.93 \pm 3.02$ m) and aspen snags ($\mathbf{\tilde{x}} = 19.72 \pm 5.66$ m) in nest plots were taller than live aspen trees (f = $20.73 \pm$ 2.62 m) and aspen snags ($\bar{x} = 16.78 \pm 5.29$ m) in non-use plots outside the nest drainage (P <0.05). Live aspen trees were of greater diameter (P < 0.05) on nest plots (f = 37.15 ± 8.15 cm) than on non-use plots within ($\bar{x} = 35.20 \pm 6.40$ cm) or outside the nest drainage ($\bar{x} = 34.62 \pm$ 7.35 cm). Diameter of aspen snags was greater (P < 0.05) on nest plots ($\ddot{x} = 37.18 \pm 7.99$ cm) than on non-use plots outside the nest drainage $(\bar{x} = 32.61 \pm 6.42 \text{ cm})$. The height and diameter of conifer snags and other deciduous snags was similar (P > 0.1) among nest and non-use plots. Thus, both live and dead aspens were generally taller and larger in dbh on nest plots than on non-use plots.

HSI ratings were greater (f = 0.934 ± 0.117 ,

range = 0.534 - 1.000) for nests than for non-use sites outside of the drainages ($\mathbf{\tilde{x}} = 0.650 \pm 0.341$, range = 0-1.000), but HSI ratings for nest sites did not differ from non-use sites within the drainage ($\bar{x} = 0.790 \pm 0.288$, range = 0–1.000) (Table 1). The model produced some inappropriate ratings for all 3 types of plots. Of the 33 nest sites, 31 received an optimal rating (HSI \geq 0.7), two received a marginal rating (0.7 > HSI> 0.4), and none received an unsuitable rating (≤ 0.4) . Of the 33 non-use plots within the same drainage as a nest plot, 24 received optimal ratings, five received marginal ratings, and four received unsuitable ratings. Of the 33 non-use plots outside of nest drainages, 18 received optimal ratings, seven received marginal ratings, and eight received unsuitable ratings. Thus, 63.6% of the plots not used for nesting were misclassified as optimal plots.

The HSI rating was primarily influenced by the density of snags (r = 0.87, n = 99, P < 0.0001), but also by canopy cover (r = 0.83, n = 99, P < 0.0001). The percent canopy dominated by aspen (r = 0.18, n = 99, P = 0.083) and the diameter of "overstory" aspen trees (r = 0.14, n = 99, P = 0.180) did not influence HSI ratings.

Nest success was high with only 1 nest failing. **Mayfield** estimates of nesting success (Mayfield 1961, 1975; Hensler and Nichols 1981) were 0.0014 daily mortality (n = 724 nest days) and 93.2% nest success. Density of aspen snags was low (1.3 aspen snags/ha) at the failed nest site.

DISCUSSION

Our data support the findings of Thomas et al. (1979b) that Williamson's sapsuckers nest in snags at the bottom of drainages within mixed-

conifer stands. Previous studies also indicated they preferred nesting in aspen trees (Hubbard 1965, Tatschl 1967, Erskine and McLaren 1972, Crockett and Hadow 1975, cf. Thomas et al. 1979*a*), but few (Li and Martin 1991) showed such strong preference for dead trees. Crockett and Hansley (1977) observed Williamson's sapsuckers nesting in live aspen most frequently, but failed to document availability of snags. In our study, no nests were located in conifer snags despite their being as abundant as aspen snags; sapsuckers may only nest in conifer snags when aspen snags are unavailable (Crockett and Hadow 1975).

Sapsuckers in our study preferred to nest in tall aspen snags, and nests were placed higher in taller trees. Low nests ($\bar{x} = 2.4$ m, range = 0.9–5.1 m) in relatively small-diameter trees (\bar{x} = 23.5 cm, range = 18-32.4 cm) documented in previous studies (Crockett and Hadow 1975) probably reflect a limited availability of large snags. Indeed, Crockett and Hadow (1975) stated that the upper dbh range of nest trees reflected the maximum available on their study site. Additionally, nest height was much higher (range = 4.0-16.9 m) in 2 other areas that they studied where sapsuckers nested in larger diameter (range = 22.5 - 41.6 cm) trees. Lower nest height is commonly associated with greater risk of nest predation for cavity-nesting birds and, hence, birds prefer to nest high when possible (Nilsson 1984, Li and Martin 1991). Birds may be forced to nest lower when using small-diameter trees to assure stability and insulation, while retaining adequate cavity size. Such responses may increase predation rates, but other studies have not measured nesting success. Moreover, the preference for south-facing nest holes found in other studies (Lawrence 1967, Crockett and Hadow 1975) may be a facultative response to suboptimal nest site quality and reduced insulative capacity in small-diameter trees. The lack of an orientation preference in our study may then reflect that birds are using high quality trees that do not require such behavioral compensations. Indeed, the high nesting success (93.2%) found in this study and on these sites previously (Li and Martin 1991, Martin and Li 1992) suggests that these are high quality nesting sites.

Characteristics of the nest tree are not the only factors influencing nesting use and success; habitat in the area surrounding a potential nest tree also influences both use and nesting success (Martin 1988b, Martin and Roper 1988, Finch 1989, Sedgwick and Knopf 1990, Li and Martin 1991). In our study, nest sites had higher densities of snags than non-use sites (Smith 1982, Li and Martin 1991). Plots within nest drainages also had higher densities of live aspen trees than non-use plots outside of nest drainages, indicating that sapsuckers may select breeding territories based on the numbers of potential nest sites (Flack 1976; Martin and Roper 1988; Martin 1988b, 1992; Li and Martin 1991). Increases in the numbers of potential nest sites (more snags) may decrease the probability of predation by causing predators to search more empty sites without reward (Martin 1988b, 1992; Martin and Roper 1988; Li and Martin 1991). Nest predators for cavity-nesting birds in our study area included house wrens (Troglodytesaedon), red squirrels (Tamiasciurus hudsonicus), and gray-collared chipmunks (Tamias cinereicollis) (Martin 1988b; T. E. Martin, pers. observ.).

Total snag density at nest sites was 7.7 snags/ ha, which exceeds the 3.7/ha thought necessary to support maximum populations of nesting Williamson's sapsuckers (Thomas et al. 1979a) and also exceeds the 5 snags/ha commonly used in forest management plans. In addition, nonuse plots within drainages had higher snag densities than non-use plots outside of drainages. Such differences probably explain the preference for drainages by Williamson's sapsuckers. However, non-use plots within drainages contained snag densities (5.31/ha) similar to those targeted in forest management plans, but birds chose sites within the drainages with even higher snag densities. These data emphasize that birds prefer higher densities of snags than commonly suggested in management plans.

Mean distance between actual sapsucker nests was 278 m (SD = 67 m, range = 175-375 m, n = 11 pairs) on our study area. The centers of our non-use plots were 230 m from the center of each nest plot. Consequently, our non-use plots generally were outside the adjacent sapsucker territories and we were very confident that additional sapsuckers were not nesting in our non-use plots. However, sapsucker territories may extend into our non-use plots in some exceptional cases, preventing their use by other birds. This would make our conclusions regarding optimal **sapsucker** habitat more conservative.

MANAGEMENT IMPLICATIONS

With respect to density and distribution of snags, current forest management practices may be insufficient to attain optimal conditions for cavity-nesting birds. Our data indicate that forest management should include conservation of large snags rather than simply producing a set number of snags of any size. Moreover, our data suggest that forest management plans that incorporate snag management should leave snags in clumps and at high densities (>5 snags/ha)within drainages or in low-lying areas. Concentrating snags in groups creates ideal habitat for many woodpeckers and a variety of other snag foragers and cavity-users (Thomas et al. 1979a, Raphael and White 1984, Hunter 1990, Sedgwick and Knopf 1990). Certainly, snag management should not attempt to space snags evenly throughout a forest.

The HSI model ranked nest sites higher than non-use sites, but inappropriate ratings were produced for both nest and non-use sites. The model is generous in assigning optimal ratings (20.7) to areas that were not used by sapsuckers. Indeed, the majority (64%) of non-use sites received optimal ratings. Total snag density was the largest contributor to an HSI rating. Nonuse or suboptimal plots could be more effectively categorized if the HSI model ranked both snags and live aspens by size because the birds preferred areas with particularly large snags and live aspens. Moreover, when assigning suitability ratings for snag densities, we suggest considering aspen snags separately from snags of other species. Distribution of snags within nesting territories is important in nest site selection, and future model versions should give higher ratings to areas with clumped distributions of snags.

Finally, dbh of "overstory" aspen trees had no significant influence on HSI ratings. The model defines an "overstory" aspen tree as any aspen $\geq 80\%$ of the height of the tallest tree in the stand. This condition was rarely met because our stands included much taller fir trees, so this variable often entered the model as a zero and therefore contributed little. Future model versions should be more liberal in the definition of an "overstory" aspen tree since dbh and height of aspen trees and snags did differ between nest and non-use plots when analyses were not restricted to the "overstory" criteria. Percent overhead cover contributed heavily to the HSI rating, but did not differ between nest and nonuse plots and should be de-emphasized in future model versions. We believe the HSI model for Williamson's sapsucker needs revision and should be more conservative in assigning optimal ratings.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1957. The A.O.U. checklist of North American birds. Fifth ed. Am. Ornithol. Union, Baltimore, Md. 691pp.
- BONEAU, C. A. 1960. The effects of violations of assumptions underlying the t-test. Psychol. Bull. 57:49–64.
- CLINE, S. P., A. B. BERG, AND H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44: 773–786.
- CROCKETT, A. B., AND H. H. HADOW. 1975. Nest site selection by Williamson's and red-naped sapsuckers. Condor 77:365–368.
- , AND P. L. HANSLEY. 1977. Coition, nesting, and postfledging behavior of Williamson's sapsuckers in Colorado. Living Bird 16:7–19.
- DONALDSON, T. S. 1968. Robustness of the F-test to errors of both kinds and the correlation between the numerator and denominator of the F-ratio. Am. Stat. Assoc. J. 63:660–676.
- ERSKINE, A. J., AND W. D. MCLAREN. 1972. Sapsucker nest holes and their use by other species. Can. Field-Nat. 86:357–362.
- FINCH, D. M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in house wrens. Condor 91:848–859.
- FLACK, J. A. D. 1976. Bird populations of aspen forests in western North America. Am. Ornithol. Union Ornithol. Monogr. No. 19. 97pp.
- GYSEL, L. W. 1961. An ecological study of tree cavities and ground burrows in forest stands. J. Wildl. Manage. 25:12–20.
- HAAPANEN, A. 1965. Bird fauna of the Finnish forests in relation to forest succession. I. Ann. Zool. Fenn. 2:154–196.
- HARRIS, R. J. 1985. A primer of multivariate statistics. Second ed. Academic Press, New York, N.Y. 576pp.
- HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93:42–53.
- HUBBARD, J. P. 1965. The summer birds of the forests of the Mogollon Mountains, New Mexico. Condor 67:404–415.
- HUNTER, M. L., JR. 1990. Wildlife, forests, and forestry. Prentice-Hall, Inc., Englewood Cliffs, N.J. 370pp.
- JOHNSON, N. K., AND R. M. ZINK. 1983. Speciation in sapsuckers (Sphyrapicus): I. Genetic differentiation. Auk 100:871–884.
- LAWRENCE, L. D. 1967. A comparative life-history study of four species of woodpeckers. Am. Ornithol. Union Ornithol. Monogr. No. 5. 156pp.
- LEMMON, P. E. 1956. A spherical densiometer for

estimating forest overstory density. For. Sci. 2:314-320.

- LI, P., AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.
- MARTIN, T. E. 1988a. Habitat and area effects on forest bird assemblages: is nest predation an influence? Ecology 69:74-84.
 - —. 1988b. On the advantage of being different: nest predation and the coexistence of bird species. Proc. Natl. Acad. Sci. USA 85:2196–2199.
- . 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 in J. M. Hagen and D. W. Johnston, eds. Ecology and conservation of neotropical migrant landbirds. Smithsonian Inst. Press, Washington, D.C.

 AND P. LI. 1992. Life history traits of cavity- versus open-nesting birds. Ecology 73:579– 592.

, AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51–57.

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

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

- NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15:165–175.
- RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity nesting birds in the Sierra-Nevada, California. Wildl. Monogr. 86:1–66.
- RASMUSSEN, D. I. 1941. Biotic communities of Kaibab Plateau, Arizona. Ecol. Monogr. 11:229–275.

- SAS INSTITUTE INC. 1985. SAS user's guide. Statistics. 1985 ed. SAS Inst. Inc., Cary, N.C. 956pp.
- SEDGWICK, J. A., AND F. L. KNOPF. 1990. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. J. Wildl. Manage. 54:112-124.
- SMITH, K. G. 1982. On habitat selection of Williamson's and "red-naped" yellow-bellied sapsuckers. Southwest. Nat. 27:464-466.
- SOUSA, P. J. 1983. Habitat suitability index models: Williamson's sapsucker. U.S. Dep. Inter., Fish Wildl. Serv. FWS/OBS-82/10.47. 13pp.
- TATSCHL, J. L. 1967. Breeding birds of the Sandia Mountains and their ecological distributions. Condor 69:479-490.
- THOMAS, J. W., R. G. ANDERSON, C. MASER, AND E. L. BULL. 1979a. Snags. Pages 60–77 in J. W. Thomas, ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA For. Serv. Agric. Handbook No. 553. Washington, D.C.
- , R. J. MILLER, C. MASER, R. G. ANDERSON, AND B. E. CARTER. 1979b. Plant communities and successional stages. Pages 22–39 in J. W. Thomas, ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA For. Serv. Agric. Handbook No. 553. Washington, D.C.
- ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 718pp.

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