RELATIONSHIPS OF SURROUNDING RIPARIAN HABITAT TO NEST-BOX USE AND REPRODUCTIVE OUTCOME IN HOUSE WRENS[1]

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Abstract. I assessed relationships among habitat structure, nest-site selection, and reproductive outcome of House Wrens (*Troglodytes aedon*) by establishing three nest-box grids in riparian woodlands in southeastern Wyoming. Over a 3-year period, 37% of the boxes contained House Wren nests; 20% contained unused nests built by male House Wrens; and 42% were never used by wrens. Direct discriminant analyses separated three box-use groups (unused, 1-year use, 2- to 3-year use) and three nesting outcome possibilities (failure all years, 1-year success, 2- to 3-year success) along gradients of habitat cover and foliage density. Compared with unused boxes, those selected repeatedly by House Wrens were located in habitats with sparser understories. Similarly, wrens were more likely to fledge offspring from boxes chosen in sparsely foliated habitats. I conclude that characteristics of the surrounding habitat influenced wren reproductive outcome and suggest that boxes in open habitats were actively selected based on their higher probability of success. Predation was the major cause of nesting failure. By nesting in open habitats, House Wrens may be more adept at detecting and deflecting cavity-nest intruders before nests are discovered and destroyed.

Key words: House Wren; dummy nests; foliage density; habitat structure; nest-box use; nesting outcome; predation risk; riparian woodlands; secondary cavity-nesting birds.

INTRODUCTION

Habitat features at or surrounding a nest site can significantly influence the rate of nesting success through effects on probability of predation (Westmoreland and Best 1985, Martin and Roper 1988), energy expenses related to nest or hole-entrance orientation (Inouye 1976, Walsberg 1981), and food supply (Martin 1987). If reproductive success is greater in certain habitats, then birds may use habitat features to evaluate quality of nest sites (Caccamise 1977, Montevecchi 1978, Cody 1981). In addition, females may choose mates on the basis of nest-site quality (Kendeigh 1941, Askenmo 1984, Slagsvold 1986) and, therefore, males may construct multiple nests, which offer females an assortment of nest-site alternatives (Kendeigh 1941).

In studies of secondary cavity-nesting birds using artificial nest sites, disparities in surrounding habitat structure have been used to explain patterns of nest-box occupancy, but the relationship between habitat variation and nesting success has rarely been addressed (Nilsson 1984). When nest boxes are identical in size, interior color, and hole entrance diameter (Lumsden 1986), nest sites are presumably selected on the basis of criteria external to the box itself (but see Brawn 1988). Such factors may include proximity to nesting conspecifics (Muldal et al. 1985) or environmental disturbance (Zach and Mayoh 1982), food supply or foraging substrate (Franzreb 1977, Hussel and Quinney 1987), probability of predation or competition (Nilsson 1984), features of the nest-box tree (Yahner 1983/1984), or adjacent habitat structure (Willner et al. 1983, Munro and Rounds 1985, Belles-Isles and Picman 1986a). Habitat characteristics surrounding the cavity site may be used as cues by nesting pairs to predict the likelihood of nesting success (Nilsson 1984).

Under conditions of nest-hole limitation, cavity-nesting birds have been shown experimentally to compete for nest boxes and natural tree holes (van Balen et al. 1982, Gustafsson 1988). House Wrens (*Troglodytes aedon*) are obligate cavity-nesters whose abundance can be limited by availability of nest sites (Yahner 1983/1984, Belles-Isles and Picman 1986a). Intense competition for nest sites and mates in House Wrens can lead to increased aggression, nest usurpation, bigamy, killing of adult conspecifics, or infanticide (Belles-Isles and Picman 1986b, 1987; Pic-

man and Belles-Isles 1988; Freed 1986a, 1986b). If nest sites are scarce, some individuals may be forced to select low-quality sites, and thus, nest-site preferences may be difficult to detect.

In an effort to reduce the confounding effects of interference competition on nest-site selection, I increased the availability of nest sites to House Wrens by establishing nest boxes in riparian woodlands (see also Drilling and Thompson 1984, Munro and Rounds 1985). I then assessed whether habitat features at nest boxes used by wrens differed from those at unused boxes. Further, I determined whether the same boxes selected in multiple years were more likely to contain successful nests, and if so, whether such boxes were associated with specific habitat attributes. In contrast to other studies which have examined within-year associations between habitat and nest placement (or nesting success), I defined habitat differences among nest sites based on numbers of years each box was used. Because the nest site rather than a site-shifting bird was the experimental unit, this approach proved to be effective in discerning high-quality habitats, i.e., habitats where nesting success is favored.

STUDY AREAS

Three study plots were established as grids in May 1982 in streamside habitats in Carbon County, southeastern Wyoming, at elevations ranging between 2,050 m and 2,250 m. Two plots were along the North Platte River, 13 km northwest and 21 km southeast of Saratoga, and one plot was at Rock Creek, 5 km northeast of Arlington. Narrowleaf cottonwood (*Populus angustifolia*) dominated the overstory along with scattered plains cottonwood (*P. deltoides*), quaking aspen (*P. tremuloides*), peachleaf willow (*Salix amygdaloides*), and Rocky Mountain juniper (*Juniperus scopulorum*). Midstory vegetation included bush willow species (*S. exigua, S. lasiandra, S. bebbiana, S. moniticola, S. ligulifolia*), thin-leaf alder (*Alnus tenuifolia*), mountain maple (*Acer glabrum*), river hawthorn (*Crataegus rivularis*), common chokecherry (*Prunus virginiana*), and western serviceberry (*Amelanchier alnifolia*). Understories were dominated by western snowberry (*Symphoricarpos occidentalis*), golden currant (*Ribes aureum*), gooseberry (*Ribes* spp.), cinquefoil (*Potentilla gracilis, P. fructicosa*), wild rose (*Rosa woodsii*), red raspberry (*Rubus idaeus*), red-osier dogwood (*Cornus stolonifera*), and a variety of grasses, sedges, and forbs. Shortgrass prairie interspersed with sagebrush (*Artemisia* spp.) bordered riparian woodlands.

METHODS

On each of the three plots, 21–22 nest boxes (65 boxes total) were mounted 2 m high on live deciduous trees >10 cm dbh. Boxes were placed 30–35 m apart in grids that varied in length and width owing to size of the riparian corridor. Nest boxes were built of 1.7-cm thick cedar, 14 × 14 × 28 cm in dimension, with 3.8-cm-diameter entrances and latchable top doors, and were labeled with grid coordinates. To standardize influences of solar radiation and prevailing winds on nest-box choice, I placed all boxes with their entrances facing toward the south or southeast —orientations preferred by some cavity-nesting species (Pinkowski 1976, Lumsden 1986).

I ascertained rates of box occupancy and nesting success by checking nest boxes early in the afternoon every 2–4 days from mid-May to late July of 1983, 1984, and 1985. Because individual male House Wrens frequently fill multiple cavities with twigs, the appearance of an egg was used as evidence of site selection by a nesting female. Box use by male wrens was recorded when incomplete twig nests were found but no eggs were laid. Due to the short breeding season (May through July) in these high altitude woodlands, only a few boxes were nested in twice during a single breeding season. Box reuse by the same pair of House Wrens could not be distinguished from late box settlement by a new pair. Such "second" nesting attempts were excluded from analyses to control for effects of seasonal variation on reproductive success. Boxes were cleaned out each September so that new twigs and nests were not confused with box contents from the year before.

Vegetation structure was sampled in June and July 1984 at all nest-box sites to determine if habitat variation affected nest-box choice or nesting success. The period of vegetation sampling was arbitrarily timed so that samples reflected habitat encountered between the periods of nest construction (May and June) and fledging of young (July and August). At each nest-box tree, I measured 34 habitat variables using a point-centered quarter sampling procedure (Finch 1989). Habitat features were sampled by dividing each location into four quadrants oriented by cardinal compass directions around

TABLE 1. Structural variables and transformations used in analyses.

Mnemonic acronym	Transformation[a]	Variable	Sampling method
DBH	SQRT	Tree diameter	Diameter (cm) at breast height of nearest trees (>3 cm) in each quadrant.
CANHT	RCPL	Canopy height	Mean height (m) of nearest trees (or shrubs if no trees in sample) in each quadrant.
SHHT	LN	Shrub height	Mean height (m) of nearest shrubs (>1 m tall) in each quadrant.
SHCD	LN	Shrub crown diameter	Mean diameter (cm) at widest crown of nearest shrubs (>1 m tall) in each quadrant.
SHDIS	SQRT	Shrub dispersion	Mean distance (m) to nearest shrub (>1 m tall).
VFD1	RCPL	Vertical foliage density in grass-forb layer	Mean number of vegetation contacts falling against vertical rod in <0.3-m interval.
VFD2	SQRT	Vertical foliage density in small shrub layer	Same as VFD1, but in 0.3- to 1-m interval.
VFD3	SQRT	Vertical foliage density in mid-canopy layer	Same as VFD1, but in 1- to 2-m interval.
VFD4	SQRT	Vertical foliage density in lower overstory	Same as VFD1, but in 2- to 9-m interval.
VFD5	LN	Vertical foliage density in upper overstory	Same as VFD1, but in >9-m interval.
EVH	LN	Effective vegetation height	Height at which a 20-cm-wide board is >90% obscured by vegetation at a distance of 5 m (Wiens 1969).
WILL	SQRT	Percent willow	Proportion of shrub species in distance sample that are willows.
SAP	LN	Percent saplings	Proportion of plant species in shrub distance sample that are saplings (<3 cm dbh).
BARE	SQRT	Percent bare ground	Percent of surface that is bare, or covered with litter, measured with ocular tube (James and Shugart 1970).
HERB	SQRT	Grass-forb ground cover	Percent cover of grasses and forbs measured with ocular tube (James and Shugart 1970).
LOGS	SQRT	Log cover	Percent cover of logs (>3 cm diameter) measured with ocular tube (James and Shugart 1970).
SHRUB	LN	Shrub cover	Percent cover of small shrubs (<1 m tall) measured with ocular tube (James and Shugart 1970).
COVER	SQRT	Live and dead woody cover	Percent cover of woody plants, saplings, and downed logs measured with ocular tube (James and Shugart 1970).

[a] Acronyms for variable transformations are defined as: SQRT = square root; RCPL = reciprocal; LN = natural log.

the nest-box tree. Pearson's product-moment correlations were used to assess relationships among habitat variables. Sixteen of the original variables were deleted from the analyses because they were either invariant or highly correlated with other variables. Within highly correlated variables, those having a sampling distribution most closely approaching normality were retained (18 variables, Table 1). Degree of normality was determined by examining normal probability plots (Afifi and Clark 1984).

DATA ANALYSES

Chi-square analysis was used to test whether the frequency of nest-box use and reproductive suc-cess differed among years. Four levels of box use were identified: (1) nest boxes never used by wrens in all three study years (NO); (2) boxes used only by male wrens for stuffing twigs, i.e., dummy nests (M); (3) boxes selected by nesting pairs during one study year (1YR); and (4) boxes used by nesting pairs for 2 or 3 years (23YR). Reproductive outcomes were classified as: (1) boxes with nesting wrens that failed to fledge offspring all years of use (F); (2) boxes that successfully fledged at least one wren in one study year (S1); and (3) boxes that fledged wrens in 2–3 years (S23). Predation was assumed if nest material was disturbed, eggs were broken, nestlings were partially eaten, predator feces were found in the

nest, eggs or nestlings were on the ground, boxes were damaged or unlatched (probably by raccoons, *Procyon lotor*), or nests were empty before nestlings were due to fledge. Nests were considered abandoned if nest contents failed to hatch or fledge, and adults were no longer active at the nest. Partial losses of clutches and broods were common, resulting from egg puncturing by conspecifics, hatching failure, and nestling starvation. Nests in reduced broods were considered successful if the nest remained active to the time of fledging.

Multivariate techniques were applied in this study because habitat gradients and relationships among multiple treatments and multiple habitat factors are not readily detected or interpretable using univariate statistics (Green 1979, Klecka 1980). To counteract the criticism that multivariate tests are prone to produce significant results even when data contain no relationships (Rextad et al. 1988), I first determined that, within a set of univariate tests, the number of variables that differed significantly was greater than that expected by chance ($P < 0.05$). For example, for a set of 18 habitat variables, the number of variables expected to differ by chance alone is $18 \times 0.05 < 1.0$. Individual habitat features were compared among use groups using randomized complete block analysis of variance (ANOVA), with the three study plots serving as blocks and the box site representing the experimental unit ($n = 65$). This design improves the accuracy of the comparisons between use classes by eliminating the variability among plots (Montgomery 1984) that may arise due to differences in wren or predator densities, and habitats.

I applied multivariate analysis of variance (MANOVA) to assess whether habitat centroids differed among box-use groups or nesting outcomes (Marascuilo and Levin 1983). Direct discriminant analysis (DA) with orthogonal rotation (VARIMAX solution, SPSS, Klecka 1975) was used to separate and classify nest-box use or fledging success along axes of habitat structure. To compensate for unequal sample sizes among groups, I based prior probabilities for classification on proportions of cases within each group. Habitat variables were selected for direct DAs based on significance levels ($P < 0.1$) of the 18 transformed variables used in the univariate block ANOVAs of box use. Additional variables used in direct DAs were those identified by stepwise DA using the Mahalanobis distance criterion for maximizing separation of groups (Klecka 1975). Thirteen habitat features were selected for the multivariate analyses of box-use groups and nine variables were selected for the analyses of reproductive outcomes. Based on univariate tests indicating habitat similarity between unused boxes and boxes with dummy nests, I created a new use class (NM) by adding the sample of dummy-nest boxes to the unused group; this consolidation improved sample size. Sufficient sample size was defined using Klecka's (1980) criteria that each group n must be at least two times greater than the number of variables.

Box's modification of Bartlett's test was used to evaluate the homogeneity of variance-covariance matrices (Williams 1983). Because Box's test is conservative (Green 1979), I used an alpha level of 0.01 to determine if covariance matrices differed. Discriminant functions were tested for statistical significance ($P < 0.05$) by transforming Wilk's lambda into a Chi-square statistic (Marascuilo and Levin 1983). Tukey's procedure for hypothesis testing (Dunnett 1980) was used to determine the significance ($P < 0.05$) of group separation of mean discriminant scores upon each individual discriminant axis. The original cases were classified into membership groups to check the adequacy of the discriminant functions (Hand 1981, Williams 1983).

Three sets of data using raw, log-transformed (LN), and a combination of square root (SQRT), reciprocal (RCPL), and log-transformed variates (Kleinbaum and Kupper 1978) were analyzed. Results using a combination of transformed variates were reported for subsequent analyses because they most closely adhered to statistical assumptions of normality and equality of covariance matrices. For ease in interpreting variables, mean values of raw data were given.

RESULTS

House Wrens nested in 21 boxes (32% of 65) in 1983, 29 (45%) in 1984, and 23 (35%) in 1985 (Table 2). Male wrens deposited twigs into an additional 15 boxes (23%) in 1983, 13 (20%) in 1984, and 11 (17%) in 1985. Over the 3-year period, 43% of all boxes were not used by wrens, 20% had male dummy nests, and 37% contained true wren nests.

Occupancy rates of boxes on each plot did not differ among years for nesting wrens ($\chi^2 = 1.27$, df = 4, $P > 0.75$), male wrens ($\chi^2 = 6.29$, df =

TABLE 2. Frequency of nest-box use and nesting success, and rates of box occupancy (% use by plot) and success (% nests that fledged ≥ one nestling) of House Wrens on three study plots in 1983, 1984, and 1985.

Year and plot	Unused boxes (%)	House Wren use		
		Male (%)[a]	Nest (%)	Success (%)[b]
1983				
Foote Camp	9 (40.9)	6 (27.3)	7 (31.8)	7 (100)
Treasure Island	14 (66.7)	2 (9.5)	5 (23.8)	5 (100)
Rock Creek	6 (27.3)	7 (31.8)	9 (40.9)	8 (88)
1984				
Foote Camp	10 (45.5)	3 (13.6)	9 (40.9)	1 (11)
Treasure Island	7 (33.3)	5 (23.8)	9 (42.9)	8 (89)
Rock Creek	6 (27.3)	5 (22.7)	11 (50.0)	9 (82)
1985				
Foote Camp	7 (31.8)	5 (22.7)	10 (45.5)	6 (60)
Treasure Island	11 (52.4)	5 (23.8)	5 (23.8)	4 (80)
Rock Creek	13 (59.1)	1 (4.5)	8 (36.4)	5 (63)
Grand total	62	39	73	53 (73)

[a] Male use was counted when a box was filled with twigs but no eggs were laid.
[b] Number of successes is the number of used boxes that fledged at least one offspring.

4, $P > 0.25$), and nesting wrens and male wrens combined ($\chi^2 = 4.26$, df $= 4$, $P > 0.50$) (Table 2). Box occupancy was dependent on whether the same boxes were occupied the preceding year (1984: $\chi^2 = 14.81$, df $= 4$, $P = 0.005$, and 1985: $\chi^2 = 16.06$, df $= 4$, $P = 0.003$). House Wrens fledged offspring from 53 of 73 nests (73%) over the 3-year period. The rate of nesting success decreased from a plot average ($\bar{x} \pm$ SD) of 96.0 $\pm$ 6.9% in 1983 to 60.7 $\pm$ 43.2% in 1984 and 67.7 $\pm$ 10.8% in 1985 (Welch's $F = 6.6$, $P = 0.08$). Boxes containing successful nests in 1983 were more likely to be used in 1984 by either the same or different birds, whereas unused or failed boxes were not likely to be occupied the following year ($\chi^2 = 9.41$, df $= 2$, $P = 0.009$). Box use in 1985 was similarly related to previous reproductive success ($\chi^2 = 10.98$, df $= 2$, $P = 0.004$).

UNIVARIATE TESTS OF BOX USE

Thirteen boxes were never used by wrens; eight boxes held only dummy nests built by male wrens; 21 boxes were occupied by nesting wrens in 1 year only; and 23 boxes had true wren nests during 2 or 3 years. Boxes containing male dummy nests were located in habitats similar to those in which boxes were never used (17 of 18 habitat features, $P > 0.05$); therefore, in multivariate analyses, these two classes were combined (NM). In pairwise comparisons, 13 features differed between various combinations of wren-use classes (NM vs. 1YR, NM vs. 23YR, 1YR vs. 23YR)

(Table 3). Because the number of features expected to differ by chance alone was less than 1 at the alpha level of 0.05, I concluded that patterns of box use were significantly related to habitat differences and that the use of multivariate tests was appropriate in subsequent analyses.

In general, trends detected using univariate tests were similar to those found in multivariate analyses so univariate results are only briefly described. In sum, nesting wrens selected boxes in one or more years in areas with smaller trees, fewer and larger shrubs, fewer saplings, and more open (herbaceous rather than woody) ground and understory cover than areas containing unused boxes.

DISCRIMINANT ANALYSIS OF BOX USE

An overall MANOVA for 13 variables and three box-use levels (NM, 1YR, 23YR) indicated that the habitat centroids significantly differed among use groups (Hotelling's trace $= 1.54$, $F = 2.54$, $P = 0.0007$). Box's test indicated that the covariance matrices computed using transformed variables did not differ in the analyses of box use ($P = 0.056$) and reproductive success ($P = 0.250$). Discriminant analysis of 13 habitat variables produced two significant discriminant functions that distinguished among three levels of box use by House Wrens (Table 4). The first discriminant function accounted for 48% of the variance and was most highly correlated with SAP, SHDIS,

TABLE 3.   Means± CL of 18 habitat features measured at nest boxes never used by House Wrens in all three study years (NO); used only by male wrens (M); used as a wren nest site in 1 year (1YR); or used as a wren nest site in 2–3 years (23YR). Total sample size = 65.[a]

| | Box-use classes | | | | | | | | |
| Habitat feature | No use all years (NO) (n = 13) | | Male use (M) (n = 8) | | Nest 1 year (1YR) (n = 21) | | Nest 2–3 years (23YR) (n = 23) | | Compari- sons[b] |
	$\bar{x}$	CL	$\bar{x}$	CL	$\bar{x}$	CL	$\bar{x}$	CL	
DBH (cm)	27.6	7.2	34.3	14.6	23.7	5.2	24.4	4.6	C
CANHT (m)	11.4	3.2	13.1	8.1	9.7	2.7	10.3	3.8	C
SHHT (m)	1.9	0.5	1.9	0.4	2.4	0.7	2.1	0.4	NS
SHCD (cm)	120.3	38.4	107.2	54.5	149.7	28.6	148.7	23.2	D
SHDIS (m)	2.9	1.6	4.0	5.6	5.8	1.9	5.3	1.8	CD
VFD1 (no. hits)	1.5	0.6	2.2	0.6	1.8	0.5	2.5	0.7	ABD
VFD2 (no. hits)	0.8	0.7	0.3	0.3	0.4	0.2	0.5	0.3	NS
VFD3 (no. hits)	1.0	0.6	0.7	0.4	1.0	0.6	1.1	0.4	NS
VFD4 (no. hits)	3.3	1.0	3.8	1.4	5.1	1.4	3.5	0.8	BC
VFD5 (no. hits)	0.8	0.6	0.7	0.7	1.3	0.9	0.5	0.4	BD
EVH (m)	1.0	0.5	0.6	0.5	0.4	0.3	0.4	0.2	D
WILL (%)	9.6	9.8	15.6	19.2	3.6	4.1	10.9	8.5	B
SAP (%)	4.8	5.0	6.3	7.9	1.8	3.7	0.5	1.1	CD
BARE (%)	28.8	15.6	21.9	16.8	26.7	12.0	23.3	10.9	NS
HERB (%)	44.2	18.0	56.4	19.7	61.6	10.8	64.8	11.2	CD
LOGS (%)	3.8	3.7	6.3	7.9	5.8	4.2	2.8	2.3	NS
SHRUB (%)	18.2	13.5	9.3	14.5	4.2	3.3	8.6	5.3	C
COVER (%)	26.8	13.9	21.8	16.7	11.8	6.1	11.9	5.3	CD

[a] See Table 1 for descriptions of habitat acronyms. Data were backtransformed for ease of interpretation.
[b] Habitat features were statistically compared among use classes using randomized block ANOVA. The classes NO and M differed in only one feature so a new class NM was formed. Habitat features that differed significantly ($P < 0.1$) between classes are indicated by: A = NO vs. M, B = 1YR vs. 23YR, C = NM vs. 1YR, and D = NM vs. 23YR. NS = not significant.

SHCD, and HERB (Fig. 1). This function, which described a situation where percentage saplings decreased as shrub dispersion, shrub size, and herbaceous cover increased, distinguished un-used boxes from those occupied by nesting wrens. Wrens avoided boxes positioned in habitats with dense sapling-small shrub understories but fre-quently nested in boxes at sites with open, her-baceous ground cover and dispersed large shrubs. Pairwise comparisons using Tukey's test indi-cated that the means of discriminant scores of used and unused box sites were significantly sep-arated on the first discriminant function (Table 5).

The second discriminant function explained 34% of the variance among groups and repre-sented a gradient of decreasing foliage density at the ground level with increasing foliage density in the overstory. Means of boxes used 2–3 years by wrens were significantly separated on the sec-ond function from means of boxes used 1 year as well as from means of boxes that failed (Table 5). Apparently, boxes placed in locations with denser overstory cover and thinner ground fo-liage were more often used as nest sites for 1 year rather than for 2 or 3 years. DA correctly clas-sified 78.5% of all boxes.

DISCRIMINANT ANALYSIS OF NESTING SUCCESS

An overall MANOVA for nine habitat variables and three nesting outcome levels indicated that the habitat centroids were significantly different among outcomes (Hotelling's trace = 1.55, F = 2.33, $P = 0.009$) in House Wrens. Two significant discriminant functions distinguished among three outcome levels in DAs of nine variables (Table 4). The first function accounted for 44% of the total variance and was most highly correlated with VFD5 and VFD1 (Fig. 2). This function

TABLE 4.   Two discriminant function analyses dis-tinguishing among nest-box use categories and repro-ductive outcomes in House Wrens.[a]

| | Box use | | Nesting outcome | |
Characteristic	Function 1	Function 2	Function 1	Function 2
% variance	48.133	34.087	44.259	34.640
χ^2	60.123	23.353	37.370	15.742
df	26	12	18	8
P	0.000	0.025	0.005	0.046

[a] Use categories in House Wrens are (1) box empty or used by male wrens in all study years, (2) box used by females in 1 year, and (3) box used by females in 2–3 years. Outcome groups are (1) failed in all years, (2) fledged at least one young in 1 year, and (3) fledged at least one young/year in 2–3 years.
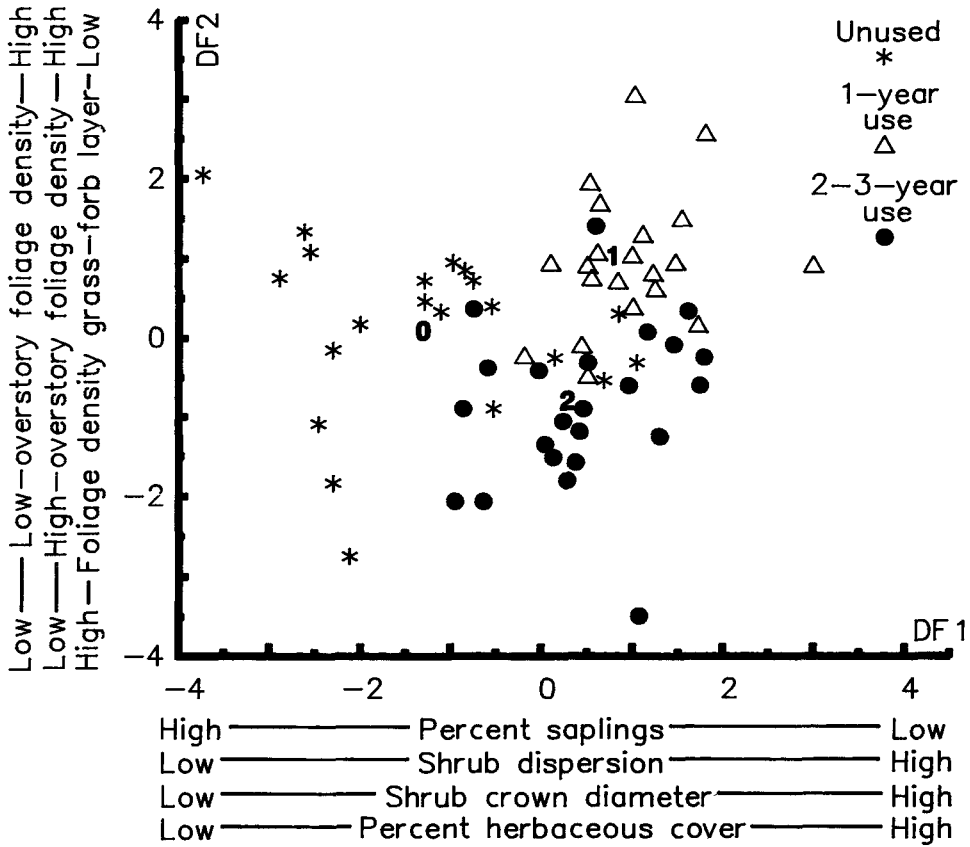
FIGURE 1.   Discriminant scores on two axes derived from discriminant analysis of box-use groups in House Wrens. Mean vectors for each group are labeled as 0 = unused, 1 = 1-year use, 2 = 2- to 3-year use. Habitat variables, used to interpret group positions, are described in Table 1.

significantly separated boxes with nesting attempts that always failed from those with successful outcomes one or more times (Table 5). Compared with successful boxes, failures were associated with denser overstory foliage, sparser herbaceous foliage in the surface layer, and higher cover of logs >3 cm diameter.

The second discriminant function accounted

TABLE 5.   Group means and pairwise comparisons of discriminant functions, prior probabilities, and classification rates from two sets of discriminant analyses that separated patterns of nest-box use or fledging success in House Wrens.

Group	n	Prior probability	Function 1 Tukey[a]	Function 1 $\bar{x}$	Function 1 SD	Function 2 Tukey[a]	Function 2 $\bar{x}$	Function 2 SD	% correctly classified[b]
Box use									
Unused all years	21	0.32	A	−1.39	1.21	A	0.03	1.10	76.2
Nest 1 year	21	0.32	B	0.87	0.70	B	0.93	0.90	85.7
Nest 2–3 years	23	0.35	B	0.38	0.88	C	−0.87	0.99	73.9
Nesting outcome									
Failure all years	11	0.25	A	1.14	1.04	A	0.75	0.68	81.8
Success 1 year	19	0.43	B	0.15	1.05	B	−0.80	1.26	68.4
Success 2–3 years	14	0.32	C	−1.12	0.89	A	0.50	0.80	78.6

[a] Pairwise comparisons of mean discriminant scores of use and outcome classes were assessed using Tukey's multiple comparison test (Dunnett 1980). Significant ($P < 0.05$) differences between means are indicated by different letters (e.g., A vs. B vs. C).
[b] Percentage of cases that were correctly classified by the discriminant analyses.
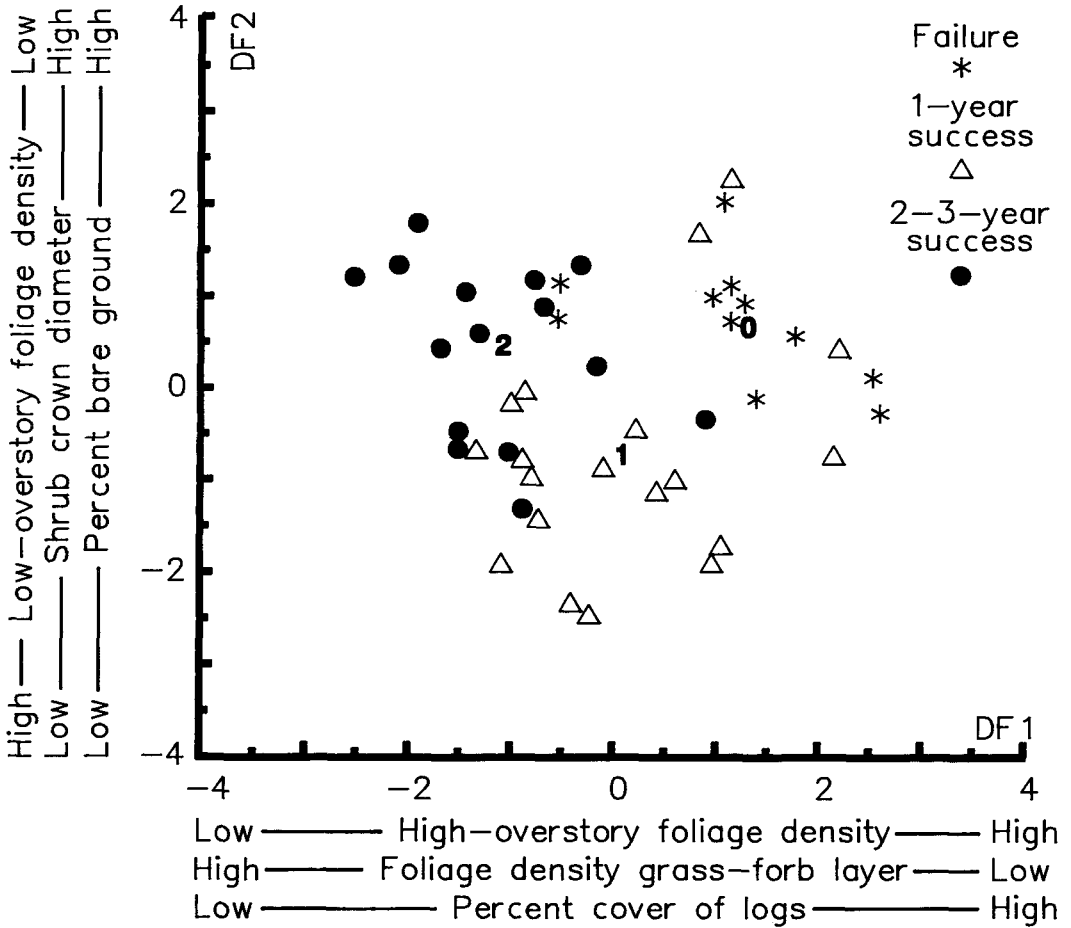
FIGURE 2. Distribution of discriminant scores on two functions, based on the analysis of nesting outcomes in boxes selected by House Wrens. Mean vectors for each group are labeled as 0 = failure, 1 = 1-year success, and 2 = 2- to 3-year success. Habitat variables, used to interpret group positions, are described in Table 1.

for 35% of the total variance in the House Wren DA and significantly distinguished between boxes with 1 year successes and boxes with either failed attempts or 2–3 year successes (Tables 4 and 5). This result suggested that successful outcomes in reused boxes were more likely to be repeated in habitats where ground surfaces were bare, shrubs large, and lower overstories (VFD4) sparse (Fig. 2). When both functions are taken into account, wrens were most reproductively successful if they selected boxes in habitats with open canopies and open surfaces with few decaying logs or dwarf shrubs. The probability of failure was greatest in habitats with thick canopy foliage and heavy nonherbaceous ground cover. In this DA, a total of 75% of 44 outcomes was correctly classified (Table 5).

DISCUSSION

NEST-BOX SELECTION BY HOUSE WRENS

Boxes used by House Wrens for nesting differed from unused boxes in that they were located in open habitats. In experimental woodlands of Pennsylvania and natural woodlands of the Midwest and central Rocky Mountains, House Wrens were reported to be abundant in areas with low shrub cover and foliage density (DeGraaf 1987, Sedgwick and Knopf 1987), selecting natural cavities in smaller trees and snags than those used by larger cavity-nesting species (Stauffer and Best 1982, Gutzwiller and Anderson 1987). In other nest-box studies, House Wrens showed the same tendency to select boxes in sparser vegetation (Belles-Isles and Picman 1986a) and, when

given a choice between boxes in logged or un-logged stands, selected more boxes in logged areas with greater herbaceous cover and fewer shrubs and saplings (Drilling and Thompson 1984). In areas with more open field and pasture, however, wrens chose boxes closer to trees, saplings, and shrubs (Willner et al. 1983, Munro and Rounds 1985). Thus, over a gradient of habitats ranging from open fields to dense, deciduous forests, House Wrens apparently select intermediate sites.

House Wrens forage on the ground and in the grass-forb-shrub layer (DeGraaf et al. 1985, Sedgwick and Knopf 1987) and may be attracted to nesting habitats with accessible surfaces for foraging, particularly if litter and herbaceous vegetation have more insects preferred by wrens. Increased foraging by House Wrens in logged and burned areas (Franzreb 1977) suggests selection for open foraging substrate with herbaceous ground cover. Boxes placed in sparse vegetation receive greater solar radiation (McComb and Noble 1981), so microclimate may play an additional role in nest-box choice, particularly in the unpredictable, high altitude climate of Carbon County, Wyoming. Alternatively, box selection may be frequency dependent (Brawn 1988). For instance, if boxes in open habitats are more easily found, then such highly visible boxes may be selected more often by wrens.

Male wrens constructed dummy nests in more varied sites than those ultimately selected by females. Boxes containing unused dummy nests were located in habitats similar to those where boxes remained empty all 3 years. Indeed, habitat structure sampled at centers of male-defended territories was similar to that at randomly sampled sites (Finch 1989), suggesting that territory selection by male wrens is nonspecialized. Male House Wrens are aggressively territorial (Kendeigh 1941) and could easily defend several boxes given the box-spacing pattern in this study (pers. observ.). Nonspecialized use of boxes by multiple-nest males may be adaptive under the following circumstances. By building nests in multiple boxes within its territory, a male may improve its chances of attracting a mate (Kendeigh 1941), even if some boxes are positioned in low-quality sites. By mating with a multiple-nest male, a female House Wren can readily renest in a surplus nest hole if the first attempt fails because of nest usurpation or predation. High densities of dummy nests may also protect the actual nest site from search-strategy predators,

as was demonstrated for the Marsh Wren, *Cistothorus palustris* (Leonard and Picman 1987).

NESTING SUCCESS IN HOUSE WRENS

Factors affecting nesting success, such as food supply, microclimate, and predation, can be influenced by habitat features at the nest site (Walsberg 1981, Westmoreland and Best 1985, Martin 1987). In this study, I focused on habitat factors that may limit predation risk because nest predation was the major source of nesting failure and failure was associated with habitat characteristics. Previous research on open-nesting birds has shown that increased foliage density may reduce risk of nest discovery by concealing the nest (Nolan 1978, Murphy 1983, Westmoreland and Best 1985), impeding predator travel or transmission of cues (Bowman and Harris 1980), or increasing the number of possible nest sites a predator must inspect (Martin and Roper 1988).

Reproductive success of House Wrens in Wyoming was associated with nest sites surrounded by sparse vegetation and little downed wood, rather than dense foliage and ground cover. Although few studies of cavity-nesting birds have considered habitat influences on reproductive outcome (see Nilsson 1984), Belles-Isles and Picman (1986a) reported that productivity of box-nesting wrens in Ontario, Canada, was greater in open habitats because nest losses to predators were minimized.

Over the 3-year period of this study, 18 of 20 unsuccessful nests were destroyed by predators, and two were deserted after partial clutches disappeared. At least four of the depredated nests showed signs of destruction by House Wrens. Evidence of conspecific intrusion included punctured eggs, nest material pulled through entrance holes (see Belles-Isles and Picman 1986b), and observations of box entry by more than two wrens (all box users viewed simultaneously in vicinity). Conspecifics are reportedly major nest destroyers in House Wrens, pecking eggs and nestlings to death to confiscate nest sites or mates, or to enhance sexual receptivity in females, allowing forced extra-pair copulations by males (Belles-Isles and Picman 1986a; Freed 1986a, 1986b; Quinn and Holroyd 1989). Predators in this study were undoubtedly small (limited by the 3.8-cm hole entrance) and possibly accustomed to entering dark cavities because of their own nesting habits. Small cavity-nest predators typically include woodpeckers and mice (Nilsson 1984), sec-

ondary cavity-nesting birds (Freed 1987, Butler and Campbell 1987), weasels (Dunn 1977), and snakes (Nolan 1959). In riparian habitats of northcentral Wyoming, bullsnakes (*Pituophis melanoleucus sayi*) and long-tailed weasels (*Mustela frenata*) were detected entering and destroying House Wren nests (L. Scott Johnson and Henry Kermott, pers. comm.). Both of these vertebrate species were observed in my study areas. Because the contents of some wren nests in this study were removed without disturbance to nesting material, the tree-climbing bullsnake is a suspected predator. Large predators include mammals able to open a box (e.g., unlatched boxes and tracks in the vicinity implicate raccoons in this study) or poke a sweeping paw through an entrance (e.g., red squirrel, *Tamiasciurus hudsonicus,* filmed by the author with time-lapse camera).

The restless activity and vociferous chatter and song of House Wrens may attract predators to nest sites (see also Skutch 1949, Willis 1973). Cavity nests may be easily approached by predators and conspecifics if dense foliage and downed logs conceal their approach from nesting adults (Belles-Isles and Picman 1986a). For the nonsedentary House Wren, the ability to detect predators first may be an important aspect of nest defense, particularly if predator visibility is greater around nest sites with little obstructive foliage. When a predator or conspecific is sighted, the nesting adults can modify their behavior accordingly, by minimizing activity at the nest, distracting the animal's attention away from the cavity, or by attacking the intruder. Direct aggression is usually effective if the intruder is a conspecific (Kendeigh 1941, Grove 1981). High visibility may actually be advantageous in territorial defense of nest sites against conspecifics.

In addition, vegetation immediately adjacent to the nest site may facilitate predation by supplying a bridge to the nest. Bullsnakes were observed entering three House Wren nests in northcentral Wyoming by descending from foliage directly above each nest box (L. Scott Johnson, pers. comm.). House Wrens may avoid nest sites where foliage is profuse if close foliage permits easier nest access by climbing snakes.

Increases in both nest-box use and nesting success of wrens were associated with open surfaces and open canopies. Thus, boxes that were occupied for multiple years were in habitats associated with greater reproductive success, sug-

gesting that boxes in open habitats were actively selected based on their higher probability of success. My results showed that box use in 1984 and 1985 was related to box occupancy and nesting outcome from the preceding year. In a study of marked birds in central Illinois, Drilling and Thompson (1988) demonstrated that female House Wrens that returned to breeding sites had produced more offspring in the previous breeding season than had nonreturning females. If nesting outcome the year before influenced rate of box reuse by returning birds in my study, then the association between multiple-year use and sparse vegetation may be an incidental result of the underlying association between nesting outcome and habitat. Hence, placement of nests by House Wrens and other bird species may ultimately depend on age and prior nesting experience (Sonerud 1985, Marzluff 1988).

LITERATURE CITED

AFIFI, A. A., AND V. CLARK. 1984. Computer-aided multivariate analysis. Lifetime Learning Publications, Belmont, CA.

ASKENMO, C.E.H. 1984. Polygyny and nest site selection in the Pied Flycatcher. Anim. Behav. 32: 972–980.

BALEN, J. H. VAN, C.J.H. BOOY, J. A. FRANEKER, AND E. R. OSIECK. 1982. Studies on hole nesting birds in natural nest sites. I. Availability and occupation of natural nest sites. Ardea 70:1–24.

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

BELLES-ISLES, J. C., AND J. PICMAN. 1986b. House Wren nest-destroying behavior. Condor 88:190–193.

BELLES-ISLES, J. C., AND J. PICMAN. 1987. Suspected adult intraspecific killing by House Wrens. Wilson Bull. 99:497–498.

BOWMAN, G. B., AND L. D. HARRIS. 1980. Effects of spatial heterogeneity on ground-nest depredation. J. Wildl. Manage. 44:806–813.

BRAWN, J. D. 1988. Selectivity and ecological consequences of cavity-nesters using natural vs. artificial nest sites. Auk 105:789–791.

BUTLER, R. W., AND C. A. CAMPBELL. 1987. Nest

appropriation and interspecific feeding between Tree Swallows, *Tachycineta bicolor,* and Barn Swallows, *Hirundo rustica.* Can. Field-Nat. 101: 433–434.

CACCAMISE, D. F. 1977. Breeding success and nest site characteristics of the Red-winged Blackbird. Wilson Bull. 89:396–408.

CODY, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. Bioscience 31:107–113.

DEGRAAF, R. M. 1987. Breeding birds and gypsy moth defoliation: Short-term responses of species and guilds. Wildl. Soc. Bull. 15:217–221.

DEGRAAF, R. M., N. G. TILGHMAN, AND S. H. ANDERSON. 1985. Foraging guilds of North American birds. Environ. Manage. 9:493–536.

DRILLING, N.E., AND C. F. THOMPSON. 1984. The use of nest boxes to assess the effect of selective logging on House Wren populations, p. 188–196. *In* W. C. McComb [ed.], Proceedings of the workshop on management of nongame species and ecological communities. Univ. of Kentucky, Lexington.

DRILLING, N. E., AND C. F. THOMPSON. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). Auk 105:480–491.

DUNN, E. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of rodents. J. Anim. Ecol. 46:633–657.

DUNNETT, C. W. 1980. Pairwise multiple comparisons in the homogeneous variance, unequal sample size case. J. Am. Stat. Assoc. 75:789–795.

FINCH, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. Ecology 70:866–880.

FRANZREB, K. E. 1977. Bird population changes after timber harvesting of a mixed conifer forest in Arizona. USDA For. Ser. Res. Paper RM-184. Fort Collins, CO.

FREED, L. A. 1986a. Usurpatory and opportunistic bigamy in tropical House Wrens. Anim. Behav. 34:1894–1896.

FREED, L. A. 1986b. Territory takeover and sexually selected infanticide in tropical House Wrens. Behav. Ecol. Sociobiol. 19:197–206.

FREED, L. A. 1987. Rufous-and-white Wrens kill House Wren nestlings during a food shortage. Condor 89:195–197.

GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York.

GROVE, P. E. 1981. The effect of location and stage of nesting on neighbor/stranger discrimination in the House Wren. Ph.D.diss. City Univ. of New York.

GUSTAFSSON, L. 1988. Inter- and intraspecific competition for nest holes in a population of the Collared Flycatcher *Ficedula albicollis.* Ibis 130:11–16.

GUTZWILLER, K. J., AND S. H. ANDERSON. 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. Condor 89:534–548.

HAND, D. J. 1981. Discrimination and classification. John Wiley and Sons, New York.

HUSSELL, D.J.T., AND T. E. QUINNEY. 1987. Food abundance and clutch size of Tree Swallows *Tachycineta bicolor.* Ibis 129:243–258.

INOUYE, D. W. 1976. Nonrandom orientation of entrance holes to woodpecker nests in aspen trees. Condor 78:101–102.

JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. Audubon Field-Notes 24:727–736.

KENDEIGH, S. C. 1941. Territorial and mating behavior of the House Wren. Ill. Biol. Monogr. 18: 1–20.

KLECKA, W. R. 1975. Discriminant analysis, p. 434–467. *In* N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent [eds.], SPSS, Statistical package for the social sciences. 2nd ed. McGraw-Hill, New York.

KLECKA, W. R. 1980. Discriminant analysis. Sage Publications, Beverly Hills, CA.

KLEINBAUM, D. G., AND L. L. KUPPER. 1978. Applied regression analysis and other multivariate methods. Duxbury Press, North Scituate, MA.

LEONARD, M. L., AND J. PICMAN. 1987. The adaptive significance of multiple nest building by male Marsh Wrens. Anim. Behav. 35:271–277.

LUMSDEN, H. G. 1986. Choice of nest boxes by Tree Swallows, *Tachycineta bicolor,* House Wrens, *Troglodytes aedon,* Eastern Bluebirds, *Sialia sialis,* and European Starlings, *Sturnus vulgaris.* Can. Field-Nat. 100:343–349.

MARASCUILO, L. A., AND J. R. LEVIN. 1983. Multivariate statistics in the social sciences. Brooks/Cole Publishing Company, Monterey, CA.

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

MARTIN, T. E., AND 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. 1988. Do pinyon jays learn from prior experience where to place their nests? Anim. Behav. 36:1–10.

McCOMB, W. C., AND R. E. NOBLE. 1981. Microclimate of nest boxes and natural cavities in bottomland hardwoods. J. Wildl. Manage. 45:284–289.

MONTEVECCHI, W. A. 1978. Nest site selection and its survival value among Laughing Gulls. Behav. Ecol. Sociobiol. 4:143–161.

MONTGOMERY, D. C. 1984. Design and analysis of experiments. John Wiley and Sons, New York.

MULDAL, A., H. L. GIBBS, AND R. J. ROBERTSON. 1985. Preferred nest spacing of an obligate cavity-nesting bird, the Tree Swallow. Condor 87:356–363.

MUNRO, H. L., AND R. C. ROUNDS. 1985. Selection of artificial nest sites by five sympatric passerines. J. Wildl. Manage. 49:264–276.

MURPHY, M. T. 1983. Nest success and nesting habits of Eastern Kingbirds and other flycatchers. Condor 85:208–219.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. Ornis Scand. 15:167–175.

NOLAN, V. 1959. Pileated Woodpecker attacks pilot

black snake at tree cavity. Wilson Bull. 71:381–382.

NOLAN, V. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. No. 26. American Ornithologists' Union, Washington, DC.

PICMAN, J., AND J. C. BELLES-ISLES. 1988. Evidence for intraspecific brood parasitism in the House Wren. Condor 90:513–514.

PINKOWSKI, B. C. 1976. Use of tree cavities by nesting Eastern Bluebirds. J. Wildl. Manage. 40:556–563.

QUINN, M. S., AND G. L. HOLROYD. 1989. Nestling and egg destruction by House Wrens. Condor 91:206–207.

REXTAD, E. A., D. D. MILLER, C. H. FLATHER, E. M. ANDERSON, J. W. HUPP, D. ANDERSON. 1988. Questionable multivariate statistical inference in wildlife habitat and community studies. J. Wildl. Manage. 52:794–798.

SEDGWICK, J. A., AND F. L. KNOPF. 1987. Breeding bird response to cattle grazing of a cottonwood bottomland. J. Wildl. Manage. 51:230–237.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

SLAGSVOLD, T. 1986. Nest site settlement by the Pied Flycatcher: Does the female choose her mate for quality of his house or himself? Ornis Scand. 17:210–220.

SONERUD, G. A. 1985. Nest hole shift in Tengmalm's Owl *Aegolius funereus* as defense against nest pre-

dation involving long term memory of the predator. J. Anim. Ecol. 54:179–192.

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

WALSBERG, G. E. 1981. Nest-site selection and the radiative environment of the Warbling Vireo. Condor 83:86–88.

WESTMORELAND, D., AND L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102:774–780.

WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. No. 8. American Ornithologists' Union, Washington, DC.

WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64:1283–1291.

WILLIS, E. O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. Auk 90:263–267.

WILLNER, G. R., J. E. GATES, AND W. J. DEVLIN. 1983. Nest box use by cavity-nesting birds. Am. Midl. Nat. 109:194–201.

YAHNER, R. H. 1983/1984. Avian use of nest boxes in Minnesota farmstead shelterbelts. J. Minn. Acad. Sci. 49:18–20.

ZACH, R., AND K. R. MAYOH. 1982. Breeding biology of Tree Swallows and House Wrens in a gradient of gamma radiation. Ecology 63:1720–1728.