THE EFFECT OF NEST PREDATION ON HABITAT SELECTION BY DUSKY FLYCATCHERS IN LIMBER PINE-JUNIPER WOODLAND[1]

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Abstract. Habitat selection by Dusky Flycatchers (*Empidonax oberholseri*) was examined in limber pine-mountain juniper (*Pinus flexilis-Juniperus scopulorum*) woodland in western Wyoming during the breeding seasons of 1986, 1987, and 1988. Vegetation characteristics associated with occupied habitat were measured (1) at the nest site, (2) within the 0.04-ha nest patch, and (3) in the breeding territory outside the nest patch; results were evaluated in relation to availability within the habitat type and nesting success. Breeding pairs of Dusky Flycatchers occupied nest patches with greater foliage cover and greater density of trees than was generally available; territories were associated with greater densities of snags and a smaller proportion of trees with dead branches extending outside the canopy than was generally available, although selectivity at the territory scale was relatively weak. Successful pairs of Dusky Flycatchers had nests with greater concealment from below, shorter distances from the nest tree to the nearest tree, and greater densities of small trees in the nest patch than unsuccessful pairs. An experiment using artificial nests suggested that concealment from below the nest site and tree density in the nest patch were selected independently. I speculate that Dusky Flycatchers select nest patches that conceal parental movements from nest predators, and that fewer trees with dead branches may indicate the selection of higher tree or foliage vigor in occupied territories. The possibility of multiple selective factors and processes, differentially affecting the selection of nest-site, nest-patch, and territory-scale habitat is discussed.

Key words: Nest predation; habitat selection; artificial nests; reproductive success; Dusky Flycatcher; Empidonax oberholseri.

INTRODUCTION

Habitat use patterns in breeding birds have commonly been attributed to the effects of habitat structure and floristics on food availability or foraging niche space (MacArthur and MacArthur 1961, Cody 1968, Holmes 1981, Wiens and Rotenberry 1981, Robinson and Holmes 1984, Rotenberry 1985, Holmes et al. 1986), with frequent support found in papers that cite food limitation or competition for food as important processes limiting reproduction in birds (Martin 1987). However, several authors have presented evidence that food may be superabundant, or competition for food non-existent, during the breeding season (Wiens 1977, Rabenold 1978, Rotenberry 1980, Anderson et al. 1982, Rosenberg et al. 1982). If food limitation exists, and habitat correlates of food availability are detectable, natural selection should favor choices of breeding territories with better foraging opportunities.

However, food is not the only potential influence on territory and habitat selection; nest pre-

dation and inclement weather may influence choice of nesting microhabitats in many bird species (Nolan 1978, Ricklefs 1969, Nilsson 1984), including tyrannid flycatchers (Murphy 1983), and may even function to decrease density-dependent nest predation at the population and community levels (Martin 1988a, 1988b). Habitat features that influence the probability of nest predation may be associated with the nest site (e.g., Calder 1973, Nolan 1978, Walsberg 1981, Murphy 1983, Stauffer and Best 1986) and the area surrounding the nest site (Petersen and Best 1985, Martin 1988c, Martin and Roper 1988).

If birds must establish territories that include particular nesting sites, microclimates, foraging space, song perches, and other requirements for reproduction (Hilden 1965), they may be forced to respond to multiple features that occur at different scales of habitat variation within a suitable habitat area. In this study, I examined habitat use by Dusky Flycatchers in limber pine-juniper woodland in western Wyoming. The objective was to describe patterns of habitat selection in relation to habitat availability and reproductive success at three spatial scales: the nest site, the nest patch (habitat surrounding the nest site), and

the territory. I tested indirectly the prediction that birds should choose breeding sites with the best foraging opportunities. To test the role of predation in determining the observed patterns of nest-site and nest-patch selection, I conducted an experiment using artificial nests.

Dusky Flycatchers (*Empidonax oberholseri*) nest throughout most of western North America in a wide variety of open habitats. Typical habitats contain dense or sparse shrub growth and scattered conifers, oaks, or deciduous riparian woodlands or thickets, often including forest edges and agricultural borders (Johnson 1963, Cornell Laboratory of Ornithology Nest Record Program). In western Wyoming, they breed in willow riparian zones where emergent conifers are present, open ecotonal woodlands of Douglas fir (*Pseudotsuga menziesii*), big sagebrush (*Artemisia tridentata*) transitions, and open mountain juniper (*Juniperus scopulorum*) and limber pine (*Pinus flexilis*)-mountain juniper woodland (pers. observ.). Previous studies in mixed conifer forest (Mannon and Meslow 1984, Morrison et al. 1986) and pinyon-juniper (*Pinus edulis-Juniperus osteosperma*) woodland (Sedgwick 1987) have considered habitat use by Dusky Flycatchers in relation to habitat availability, but no studies have evaluated habitat selection by Dusky Flycatchers in relation to reproductive success.

METHODS

STUDY AREA

The study was conducted during three breeding seasons, from 1986 through 1988, on the Whiskey Basin State Bighorn Sheep Reserve in the Wind River Range of Wyoming. A 40-ha study area was established on the south-facing (20–40%) slope of Torrey Rim, at an elevation of 2,317–2,470 m. Late May to early August temperatures occasionally reached 29°C in mid-afternoon, but sometimes dropped to below freezing at night. Late afternoon and evening thunderstorms and short periods of rain were common; occasional hail, and on one occasion, light snowfall, occurred. The topography included numerous steep, dry drainage courses, rocky outcrops, and open slopes. The vegetation consisted primarily of scattered limber pines, mountain juniper, and Douglas fir, with ground-level vegetation dominated by big sagebrush and intermixed with a variety of grasses and forbs.

Potential nest predators abundant enough to

be encountered regularly in the study area included least chipmunks (*Eutamias minimus*), Uinta ground squirrels (*Citellus armatus*), Clark's Nutcrackers (*Nucifraga columbiana*), Black-billed Magpies (*Pica pica*), and Common Ravens (*Corvus corax*). Red squirrels (*Tamiasciurus hudsonicus*), golden-mantled ground squirrels (*Citellus lateralis*), long-tailed weasels (*Mustela frenata*), and coyotes (*Canis latrans*) were also present.

VEGETATION

Vegetation structure and composition in the study area were sampled on nest-centered plots (after nesting attempts were completed) in late July/ early August of 1986, 1987, and 1988, and on randomly-selected plots in late July of 1987 and 1988. Nest-centered samples included measurements at three spatial scales: (1) nest site characteristics were measured within or below the nest tree; (2) nest patch characteristics were estimated within a radius of 11.3 m (0.04 ha) of the nest site, with sampling transects extending in cardinal compass directions from the nest site to the perimeter of the patch; (3) each territory-scale estimate was derived from four 50-m transects with centers 50 m from the corresponding nest, oriented perpendicular to the nest patch transects. All territory-scale transects were located within the territorial boundaries of the corresponding nesting pairs. I estimated territorial boundaries by observing the positions of birds that were color-banded near their nest sites. Habitat availability was measured throughout the study area along randomly selected 50-m transects oriented perpendicular to the slope and at least 50 m from adjacent transects.

Ground cover and foliage cover variables were measured by sighting vertically through an ocular tube (James and Shugart 1970) at 1-m intervals while walking along the sampling transects. Tree densities were estimated using point quarter distances (Cottam and Curtis 1956) centered at the nest site and at the mid-points of territory-scale transects and random transects, and by counting all trees by species and size class (1–2 m, 2–5 m, >5 m tall) within the 0.04-ha nest patch. Density of snags was measured within 20-m wide belts centered along random and territory-scale transects, and within the 0.04-ha nest patch. Nest concealment was measured by estimating the percent of each nest hidden by foliage when viewed from (1) below the nest (at ground

level), (2) just above the nest tree canopy, and (3) three side positions at nest height approximately 2 m from the nest (average), two perpendicular to and one in line with the axis to the center of the nest tree.

BIRDS

Censuses of all breeding bird species in the study area were conducted from 17 June through 9 July during each year of study using the spot-mapping method (Williams 1936, Kendeigh 1944). Most Dusky Flycatcher nests were found during the pre-laying or laying phase of the breeding cycle. Nesting success was monitored every three or four days, often from remote positions using binoculars to view parental activity to confirm nest survival and avoid possible influence on the probability of nest predation (Westmoreland and Best 1985, cf. Gottfried and Thompson 1978). Nesting success was evaluated using the Mayfield method (Mayfield 1975, Johnson 1979). For the purpose of the habitat selection analysis, I considered a nest successful if at least one nestling was known to have fledged or survived to the 18th day of the nestling period. I assumed predation to be the cause of nest failure if nest materials were torn or disturbed, or if the eggs or nestlings (younger than fledging age) disappeared from the nest and the area below the nest.

ARTIFICIAL NESTS

In 1988, 54 artificial nests were constructed from fine grasses found near the study area. The artificial nests were modeled after Dusky Flycatcher nests observed in previous seasons, with similar dimensions, material, and color. Thin black wire was used to strengthen the nests and to attach them to the nest trees.

The artificial nests were placed in the study area in positions defined by a preliminary stepwise discriminant analysis (SDA) of the 1986 and 1987 data. Density of trees in the 0.04-ha patch and nest height, important predictors of nest success in the preliminary analysis, were used as treatment variables. Nest concealment from above did not enter the preliminary SDA but was included as a treatment variable because of a relatively strong univariate separation of successful and failed nests ($F = 2.3$, df = 1, 17, $P = 0.16$) that was lost in the SDA because of correlations with other variables. Three values for each treatment variable were used in the systematic placement of artificial nests, encompassing

the range of values ($n = 22$) observed during the 1986 and 1987 breeding seasons (density of trees per 0.04 ha = 0–2, 5–8, >10; nest height = 0.5 m, 1.4 m, 2.3 m; concealment from above = 0%, 50%, 100%). Nest concealment from below and from the side did not enter the preliminary SDA and were not held constant in the field, but were estimated as potentially important covariables after placement of the artificial nests, using the method described above for real nests.

Because most (76%, $n = 34$) Dusky Flycatcher nests in the area were in or near dry drainage channels, artificial nests were placed along dry drainage channels throughout the study area. Other variables that were held constant during artificial nest placement, defined by average values in the 1986 and 1987 data, included distance to the edge of the canopy (0.3 m), nest tree species (juniper; 82% of 34 Dusky Flycatcher nests were in juniper), and nest support (crotch or fork with main branch diameter of 1–5 cm).

East nest was placed in the nearest appropriate location, at least 50 m from the previously placed nest, beginning at a random point in each drainage. We placed two fresh quail (*Coturnix coturnix*) eggs in each artificial nest and monitored the nest contents every 3–4 days for 14 days (the duration of incubation in Dusky Flycatchers). All artificial nests were constructed, handled, and approached directly to check for predation in an identical manner. The experiment was conducted during the period when Dusky Flycatchers were incubating in 1988, from June 22 through July 5.

STATISTICAL ANALYSES

Several of the variables were transformed to improve the normality of the data before statistical analysis. Univariate analysis of variance indicated that availability of habitat features in the study area (random plots) and most features associated with nest-site, nest-patch, and territory-scale Dusky Flycatcher habitat did not differ significantly among years ($P > 0.05$). There were no significant differences among years in the number of Dusky Flycatcher territories ($\chi^2 = 0.22$, $P > 0.89$), the overall breeding bird density ($\chi^2 = 3.89$, $P > 0.15$), or species richness of breeding birds ($\chi^2 = 0.14$, $P > 0.97$) in the study area (Kelly and Kelly 1989). Dusky Flycatcher nesting success was also similar among years (see results). Therefore, except where stated otherwise, the data were pooled across years in the analysis.

Stepwise discriminant analysis (SDA) was used to compare habitat occupied by Dusky Flycatchers with available habitat, and habitat associated with successful vs. failed Dusky Flycatcher nests. Before the SDA, product-moment correlation coefficients were calculated for all pairwise combinations of variables. In each pair with a correlation greater than 0.4, I eliminated the variable with the lowest between-group significance. The classification performance of each SDA was tested against a chance model, assuming a probability of correct classification of any group by chance proportional to group size, using Cohen's kappa and its associated Z value (Titus et al. 1984). Stepwise logistic regression (SLR), a nonlinear analysis that does not assume multivariate normality (Engelman 1988), was used to check the stability of the variables in the SDA model (Capen et al. 1986). Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to model the results of the artificial nest experiment.

RESULTS

NESTING SUCCESS

The average daily survival rates of Dusky Flycatcher nests did not differ significantly ($P > 0.05$) between incubation and nestling periods within each year, or within periods among years. However, nest survival rate was significantly greater during incubation (0.984, SE = 0.007) than during the nestling period (0.942, SE = 0.016) in the pooled three-year sample ($P < 0.05$). The probability of a nest surviving both the incubation and nestling periods, based on pooled daily survival rates within each period, was 0.35. Nineteen of 32 nests (59.4%) failed; 17 of the 19 nest failures (89.5%) resulted from predation and two nest failures (10.5%) resulted from periods of inclement weather.

HABITAT SELECTION

Univariate analyses suggested that Dusky Flycatchers selected nest patches with greater density of trees (shorter point quarter distances), greater density of snags, greater foliage cover 1–5 m above ground, less sagebrush cover, and a smaller proportion of limber pines than was available in the study area (Table 1). The mean values of most features associated with the territory outside the nest patch did not differ significantly from availability. However, the density of snags was significantly greater on occupied territories than on random plots (Table 1). Univariate habitat differences between successful and failed nests were not significant.

Habitat use by Dusky Flycatchers was best discriminated from available habitat on the study area by greater foliage cover at 1–2 m above ground in the nest patch, greater density of trees in the nest patch, and a smaller proportion of trees in the territory with dead branches extending outside the canopy (Table 2, Fig. 1). Structure correlations between canonical variable scores ($n = 88$) and original variables further characterized habitat occupied by Dusky Flycatchers as having greater foliage cover at 2–5 m above ground in the nest patch ($r = -0.62$), and greater foliage cover at 1–2 m ($r = -0.56$) and 2–5 m ($r = -0.42$) above ground in the territory than was generally available. However, foliage cover was significantly greater than availability only when measured at the nest-patch scale (Table 1). Density of snags did not enter the SDA because of correlations with other variables (structure correlation = -0.33), but in a separate SDA using only territory-scale variables, density of snags entered the function first, followed by trees with dead branches outside the canopy; snags and dead branches influenced the resulting function in opposite directions (structure correlations = -0.64, 0.41, respectively; approx. $F = 4.9$, df = 3, 84, $P < 0.005$; Cohen's kappa = 0.36, $P < 0.01$). Thus, the overall and the territory-scale SDAs suggested that Dusky Flycatchers establish territories with greater density of snags but fewer trees with dead branches outside the canopy than available, even though both variables were positively correlated over all plots ($r = 0.34$, df = 86, $P < 0.001$), random plots ($r = 0.36$, df = 52, $P < 0.01$), and occupied plots ($r = 0.51$, df = 32, $P < 0.005$). This result was also suggested by univariate comparisons (Table 1).

Successful nests were best discriminated from failed nests by having greater nest concealment from below, a shorter distance from the nest tree to the nearest tree, and a greater density of small trees (height < 2 m) in the nest patch (Table 2, Fig. 1). No other original variables were strongly associated with nest success (structure correlations $< |0.40|$).

Habitat selection in the study area was reflected in a significantly smaller generalized variance among utilized plots than among random plots, as indicated by the determinant of the within-group covariance matrix ($|\Sigma| = 0.0012$ and

TABLE 1. Means (and standard errors) of habitat variables measured at the nest site, nest patch, and within territories of Dusky Flycatchers in western Wyoming.

Variable	Random (n = 54)	Scale	Utilized[a] (n = 34)[b]	Failed (n = 19)	Successful (n = 13)
Concealment of nest from above (%)	—[c]	Site	83.44 (3.41)	79.00 (5.66)	90.08 (2.59)
Concealment of nest from below (%)	—[c]	Site	46.29 (4.56)	38.95 (5.41)	56.85 (7.94)
Concealment of nest from the side (%)	—[c]	Site	63.00 (3.51)	60.00 (4.63)	67.85 (6.23)
Direction from tree center (degrees)	—[c]	Site	163.21 (16.76)	169.37 (21.96)	154.23 (24.74)
Distance to edge of canopy (m)	—[c]	Site	0.30 (0.04)	0.30 (0.05)	0.32 (0.07)
Height of nest above ground (m)	—[c]	Site	1.33 (0.09)	1.34 (0.13)	1.25 (0.11)
Density Douglas fir per 0.04 ha	—[c]	Patch	2.32 (0.43)	1.58 (0.34)	3.08 (0.94)
Density junipers per 0.04 ha	—[c]	Patch	4.85 (0.67)	5.00 (1.02)	4.46 (0.84)
Density limber pines per 0.04 ha	—[c]	Patch	2.15 (0.44)	1.84 (0.61)	2.69 (0.73)
Density large trees (>5 m) per 0.04 ha	—[c]	Patch	1.94 (0.31)	1.90 (0.46)	1.92 (0.43)
Density small trees (<2 m) per 0.04 ha	—[c]	Patch	3.03 (0.49)	2.53 (0.71)	3.62 (0.68)
Distance nest tree to nearest tree (m)	—[c]	Patch	2.44 (0.33)	2.95 (0.53)	1.92 (0.31)
Density of snags per 0.1 ha	2.54 (0.33)	Patch	4.38 (0.50)**	4.90 (0.76)	3.54 (0.66)
		Territory	3.67 (0.44)*	3.50 (0.60)	3.46 (0.68)
Foliage cover 1–2 meters (%)	5.69 (0.79)	Patch	9.50 (0.74)***	8.79 (0.75)	9.54 (1.38)
		Territory	5.28 (0.51)	5.26 (0.69)	5.19 (0.91)
Foliage cover 2–5 meters (%)	5.70 (0.96)	Patch	10.44 (1.29)***	9.84 (1.45)	10.31 (2.58)
		Territory	5.26 (0.69)	5.18 (0.83)	5.08 (1.35)
Juniper (proportion of trees)	0.64 (0.04)	Patch	0.57 (0.06)	0.65 (0.08)	0.48 (0.11)
		Territory	0.58 (0.04)	0.61 (0.06)	0.58 (0.06)
Limber pine (proportion of trees)	0.32 (0.04)	Patch	0.18 (0.04)*	0.17 (0.05)	0.21 (0.07)
		Territory	0.28 (0.03)	0.27 (0.05)	0.28 (0.05)
Point quarter distance to trees (m)	12.80 (1.22)	Patch	6.82 (1.02)***	6.62 (0.51)	7.71 (2.59)
		Territory	12.42 (1.61)	11.73 (1.48)	13.47 (3.64)
Sagebrush cover (%)	16.48 (1.28)	Patch	11.62 (1.41)*	11.32 (2.13)	12.23 (1.95)
		Territory	15.07 (1.09)	14.97 (1.40)	14.85 (1.66)
Trees with dead branches outside canopy (proportion of trees)	0.45 (0.04)	Patch	0.39 (0.05)	0.35 (0.07)	0.39 (0.09)
		Territory	0.37 (0.03)	0.38 (0.04)	0.37 (0.06)
Tree height, mean (meters)	3.08 (0.14)	Site	3.21 (0.32)	3.32 (0.51)	3.08 (0.38)
		Patch	3.17 (0.22)	3.22 (0.30)	3.27 (0.36)
		Territory	3.16 (0.09)	3.13 (0.12)	3.14 (0.14)

[a] Significant t-tests of utilized vs. random plots indicated by: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[b] Includes two nests with unknown survival.
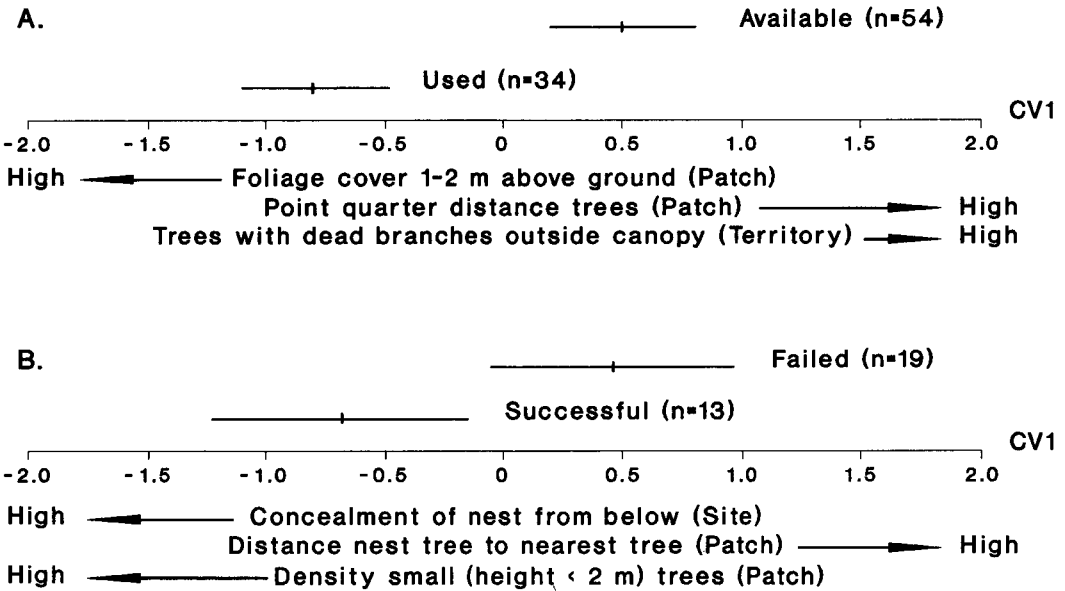[c] Availability data were not obtained.

A.

B.

FIGURE 1. Means and 95% confidence intervals of canonical variable (CV1) scores from stepwise discriminant analysis of (A) used vs. available habitat and (B) habitat associated with successful vs. failed breeding pairs of Dusky Flycatchers in western Wyoming.

0.1353, respectively; Box's M: $\chi^2 = 293.01, P < 0.001$; Morrison 1976:253). Consequently, the assumption of equality of within-group covariance matrices (Williams 1981, 1983) was not met in the SDA of used-vs.-available plots; however, the within-group covariances in the SDA of suc-cessful-vs.-failed nests were not significantly different (Box's M: $\chi^2 = 5.68, P > 0.45$). The SDA models correctly classified used-vs.-available plots and successful-vs.-failed nests 55% and 48% better than chance alone, respectively (Table 2).

Scale-specific SDAs corroborated the overall

TABLE 2. Stepwise discriminant analysis (SDA) of (A) used vs. available habitat and (B) habitat associated with successful vs. failed breeding pairs of Dusky Flycatchers in western Wyoming.

Variable—Scale	Order entered	Structure correlation	Coefficient
A. Used ($n = 34$) vs. Available ($n = 54$)			
Foliage cover 1–2 meters—Patch	1	−0.75	−0.51
Point quarter distance trees—Patch	2	0.71	2.24
Trees (proportion) with dead branches outside canopy—Territory	3	0.29	2.08
(CONSTANT)			−1.69
Wilk's Lambda		0.71	
Approximate F-statistic		11.56***	
Cohen's kappa		0.55***	
B. Successful ($n = 13$) vs. Failed ($n = 19$)			
Concealment nest from below—Site	1	−0.65	−0.03
Dist. nest tree-nearest tree—Patch	2	0.50	2.14
Density small trees (<2 m)—Patch	3	−0.43	−0.64
(CONSTANT)			−0.36
Wilk's Lambda		0.74	
Approximate F-statistic		3.29*	
Cohen's kappa		0.48**	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

results, generally identifying the same predictor variables with the same relative strengths at their respective scales, with one exception: the territory-scale SDA revealed the primary role of snag density as a predictor of utilized habitat, as noted above. Territory-scale habitat associated with successful nests could not be discriminated from habitat associated with failed nests in either the overall SDA (Table 2) or the territory-scale SDA (all F-values < 0.11; df $= 1, 30$; $P > 0.70$). Concealment from below, the only nest-site predictor of nest success in the overall SDA, entered the nest-site SDA along with concealment from above (structure correlations $= -0.80$ and -0.61, respectively; approx. $F = 3.16$; df $= 2, 29$; $P < 0.10$).

ARTIFICIAL NEST EXPERIMENT

None of the treatment effects or their interactions were significantly related to artificial nest survival when covariate terms for nest concealment from below and from the side were included in the model. However, the results were confounded by a significant negative correlation between concealment from below and density of trees in the nest patch ($r = -0.50$, df $= 52$, $P < 0.001$)—probably a result of foliage-bearing branches being shaded out at heights below 2 m in areas with greater density of trees. This contrasts with real Dusky Flycatcher nests, in which concealment from below was not correlated with tree density in the nest patch ($r = -0.08$, -0.06, 0.19, for density of small trees, distance from nest tree to nearest tree, and point-centered quarter distance to trees, respectively; df $= 32$; $P > 0.05$). After removing the covariate terms, the resulting ANOVA suggested that survival of artificial nests was significantly related to lower tree density in the nest patch ($F = 3.45$, df $= 2$, $P < 0.04$). Average daily nest survival rate was significantly lower for artificial nests (0.877, SE $= 0.016$) than for real nests (0.981 during incubation in 1988, SE $= 0.013$, $P < 0.001$).

DISCUSSION

Dusky Flycatchers were more selective at smaller scales of habitat use, i.e., at the nest site and nest patch, than at the territory scale. The overall and territory-scale analyses suggested that Dusky Flycatcher habitat included more snags but a smaller proportion of trees with dead branches outside the canopy than was generally available. By providing foraging microhabitat and song

perches, snags may be closely related to ultimate factors that influence habitat selection during territory establishment. The proportion of trees with dead branches outside the canopy was originally included in the study as a second measure of potential perching substrate for foraging or singing, but may inversely index tree or foliage vigor related to the availability of insect prey (Knopf et al. 1990). Therefore, the selection of territories with greater densities of snags and proportionally greater incidence of high vigor among living trees, as could be found in areas regenerating after fire, drought, disease, or other disturbance, might explain the results, although tree or foliage vigor was not specifically measured and my data did not allow a direct test of this possibility.

In general, little selectivity was associated with territory-scale habitat. Possible reasons for reduced selectivity include the absence of food limitation, or competition for food (Wiens 1977, 1983), prior selection of suitable habitat at the landscape (between-habitats) scale (Hilden 1965, Wiens 1985, Hutto 1985), constraints of nest-site or nest-patch selection (Alatalo et al. 1985, Morse 1985:147), and failure of birds to recognize gradients of foraging habitat quality because episodic (high-elevation) weather extremes may erode the link between proximate ques related to foraging opportunities and the ultimate availability of insect prey (Greer and Anderson 1989). Also, if food supplies exploited by Dusky Flycatchers typically change quickly over space and time because of a predominance of flying insects, the influence of habitat on food availability may be reduced. Alternatively, my methods may have failed to detect such gradients.

The present study suggests that nest concealment, especially from below the nest, is an important factor affecting nest success. The importance of nest concealment in reducing the probability of nest predation has been described for tyrannid flycatchers (Murphy 1983) and other species (Nolan 1978, Stauffer and Best 1986, Martin and Roper 1988; but see Gottfried and Thompson 1978). Two of 19 nest failures in the present study apparently resulted from extreme weather: one failed following a period of probable heat stress and one following heavy rainfall. Eckhardt (1977) witnessed the abandonment of several Dusky Flycatcher territories following a three-day June storm. Therefore, the selection of foliage cover at the nest site may be partly associated with the advantages of thermal cover

(Walsberg 1981, 1985; Murphy 1983, 1985; Sakai and Noon 1991).

The habitat selection analysis strongly suggested that tree density and foliage cover in the nest patch were positively related to habitat use and nest success. Martin and Roper (1988) found nest patch foliage to be an important factor in determining nest success in Hermit Thrushes (*Catharus guttatus*). They concluded that the primary benefit of nest patch foliage was in providing a greater number of potential nest sites that predators must examine, thus decreasing the probability of nest predation. This hypothesis is not supported by the present study on Dusky Flycatchers because (1) junipers, which were used as nest trees for 28 of 34 nests (82.4%), were less dense (although not significantly) in patches associated with successful nests than in patches associated with failed nests, (2) limber pines and Douglas fir are structurally very different from junipers with regard to potential nest-site characteristics, but occurred in greater proportions and densities (although not significantly) in patches associated with successful nests than in patches associated with failed nests, and (3) artificial nest survival was greater in nest patches with fewer trees (although nest concealment from below was also greater).

In addition to having greater tree density and foliage cover in the nest patch, successful Dusky Flycatcher nests were also associated with a shorter distance to the nearest tree beyond the nest tree than were failed nests. Concealment of parental movement in the nest patch, resulting in reduced nest-site detectability and vulnerability to predation, is one possible explanation for this result. Skutch (1949) suggested that parental activity may attract the attention of predators, although Ricklefs (1969) found little evidence to support this hypothesis. In a comparison of predation rates on artificial and natural nests in old-field habitat, Gottfried and Thompson (1978) found no relationship between nest failure and the presence of parental activity. Recently, the value of nest patch foliage cover in concealing the parental movements of Sage Sparrows (*Amphispiza belli*) was suggested by Peterson and Best (1985).

In the artificial nest experiment, the lack of parental activity may have precluded any positive effect of tree density on artificial nest survival. The resulting negative effect of tree density on artificial nest survival resulted from an inverse relationship between tree density and concealment from below. Isolated trees tend to develop more foliage on their lower branches because of greater available light levels; consequently, isolated trees provide greater nesting cover from below if selected randomly. In contrast to the artificial nest results, concealment from below Dusky Flycatcher nests was not correlated with tree density in the nest patch and successful Dusky Flycatcher nests were associated with both greater tree density in the nest patch and greater concealment from below. These results suggest that Dusky Flycatchers actively select the nest patch, then the nest site within the patch, to conceal their nests in areas with greater tree density, where parental flights are probably less conspicuous but nest concealment from below is less available.

Aggressive nest defense is characteristic of open-nesting tyrannid flycatchers (Murphy 1983). Although distraction displays by Dusky Flycatchers were observed twice by Johnson (1963), the flycatchers we observed were invariably quiet and shy around the nest. When approached, females often remained on their nests until the observer moved to within a meter or less, at which time they would make a quick, quiet, and inconspicuous exit. We never observed chases during incubation or nestling periods, except between members of a mated pair. Dusky Flycatcher behavior apparently functioned to conceal their presence in the nest patch. Bowles and Decker (1927) reported similar behavior in Dusky Flycatchers. Murphy (1983) suggested that the quiet and unobtrusive behavior of the Yellow-bellied Flycatcher (*Empidonax flaviventris*) results in predator avoidance benefits related to achieving anonymity in the vicinity of well-hidden but accessible open ground nests, where there is little chance of deterring terrestrial predators. He concluded that nest placement and behavior in the vicinity of the nest are probably co-evolved traits. The results of the present study are consistent with the hypothesis that the quiet, non-aggressive, inconspicuous behavior of Dusky Flycatchers near the nest may have co-evolved with the selection of nest-patch foliage that conceals attending flights to and from relatively accessible (1–2 m above ground) nest sites. However, the possible relationship between behavior in the nest patch and reproductive success should be further investigated.

An increase in conspicuousness of Dusky Fly-

catcher nests when both adults were making foraging flights to feed nestlings could account for the greater nest mortality rate observed during the nestling period. The greater conspicuousness of quail eggs in artificial nests, which were not covered by incubating females and sometimes protruded above the nest rim, could account for the higher mortality rate in the artificial nest experiment, although human scent or activity around artificial nest sites could also have been involved.

Martin (1988c) argued that for birds using foliage for foraging and nesting substrate, foliage density should index the availability of both insect prey and nest sites. However, species such as Dusky Flycatchers that often sally-glean or pounce on prey that occur on foliage in open areas but tend to nest in relatively dense patches of foliage, as found in the present study, may use different criteria in selecting foraging habitat than in selecting nesting habitat. Collins (1981) found that vegetation structure differed between nest and perch sites for several species of paruline warblers, and suggested that this resulted from differences in male and female foraging ecologies. Sedgwick and Knopf (1992) described sex-specific differences in habitat selection between nest and perch sites in Willow Flycatchers (*Empidonax traillii*). In the present study, female Dusky Flycatchers were observed more often near the nest site, in denser foliage, and closer to the ground than males (pers. observ.). Such differentiation in habitat use between sexes may occur if birds forage near their centers of activity, which differ during the breeding season (Morse 1968, Franzreb 1983, Holmes 1986). Morphological differences among Dusky Flycatchers reflect such differences in foraging habitat. Females have shorter, more rounded wings suitable for shorter flights in low vegetation within the nest patch, whereas males have longer, more pointed wings which are better suited for longer, more rapid flights from higher perches in open (territory-scale) habitat (Johnson 1963, Eckhardt 1979). However, similar differences in wing morphology between sexes are typical among tyrannid flycatchers (Eckhardt 1979, Pyle et al. 1987), suggesting that this difference in Dusky Flycatchers may be a phylogenetic carryover rather than a specific adaptation for foraging habitat.

Insectivorous birds probably establish breeding territories in response to combinations of processes and factors operating at local, regional, and global scales (Holmes et al. 1986), such as predation, weather, and food limitation. On the Torrey Rim study area, Dusky Flycatchers select multiple habitat features that correspond to different scales of habitat measurement around the nest site. Ecological processes that result in habitat use patterns at the local scale described by my study may not account for patterns at larger scales of habitat variation (Wiens 1981, 1983; Holmes et al. 1986; Knopf et al. 1990). Furthermore, patterns of habitat selection evident at the local scale may or may not be contingent on hierarchical responses at the broader between-habitats scale (Gutzwiller and Anderson 1987). Given the broad use of riparian, shrub, and woodland habitats by Dusky Flycatchers, a multi-scale investigation of habitat use patterns within and between habitat types would help to clarify the habitat relationships of this species.

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