

# SONG SPARROWS VS. COWBIRD BROOD PARASITES: IMPACTS OF FOREST STRUCTURE AND NEST-SITE SELECTION<sup>1</sup>

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**Abstract.** We studied Song Sparrow (*Melospiza melodia*) reproductive ecology in natural and restored riparian forest to evaluate the influence of habitat structure and nest-site selection on parasitism by Brown-headed Cowbirds (*Molothrus ater*). Logistic regression revealed that habitat structure affected the probability of parasitism at two scales, BROAD (within 11.3 m of the nest) and LOCAL (within 5 m of the nest). Nests with abundant lateral cover at a height of < 1 m (BROAD) were less likely to be parasitized, suggesting that lateral cover at ground level may reduce parasitism by concealing host movements in the vicinity of the nest. In contrast, nests with abundant foliage cover at a height of 2–3 m (LOCAL) were more likely to be parasitized, suggesting that foliage cover above the nest may increase parasitism by providing perches from which female cowbirds can watch host activities and find nests. Sparrow nest-site selection varied among forest types, but lateral cover at ground level and foliage cover above the nest were similar for nests in each forest type. Results suggest that further research on the effects of habitat structure on nest-site selection and cowbird parasitism could lead to methods of reducing parasitism through appropriate habitat management and restoration efforts.

**Key words:** brood parasitism, Brown-headed Cowbird, habitat restoration, habitat structure, *Molothrus ater*.

## INTRODUCTION

Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) may reduce reproductive success and cause population declines in some songbirds (Brittingham and Temple 1983, Robinson et al. 1995). Removal of cowbirds can reduce their impacts, but it is expensive and involves intensive, long-term effort (Rothstein et al. 1987, Rothstein and Robinson 1994). An alternative approach may be to identify structural characteristics of the habitat that minimize cowbird parasitism, and make appropriate alterations or improvements.

Susceptibility to cowbird parasitism may vary for both behavioral and ecological reasons. Host behaviors may either deter (Robertson and Norman 1977) or attract (Robertson and Norman 1977, Smith 1981) female cowbirds. Nesting birds in different habitats experience different levels of parasitism due to patterns of habitat use

by female cowbirds (Zimmerman 1983, Hahn and Hatfield 1995), degree of habitat fragmentation (Johnson and Temple 1990, Gustafson and Crow 1994), and species composition of the host community (Clark and Robertson 1978, Barber and Martin 1997). Within a particular habitat, nest-site characteristics also may influence vulnerability to parasitism (Brittingham and Temple 1996, Burhans 1997).

We use Song Sparrows (*Melospiza melodia*) to investigate the influence of habitat structure and sparrow nest-site selection on nest parasitism. Song Sparrows are frequently parasitized by cowbirds (Nice 1964, Smith and Arcese 1994), a possible factor in the decline of their populations in some areas (Rogers et al. 1997). Moreover, they may serve as a model for rare, threatened, or sensitive species such as Southwestern Willow Flycatchers (*Empidonax traillii extimus*) and Yellow-breasted Chats (*Icteria virens*) that also nest in open cup nests in the understory and utilize similar habitat. Specifically, we examine whether habitat structure at two

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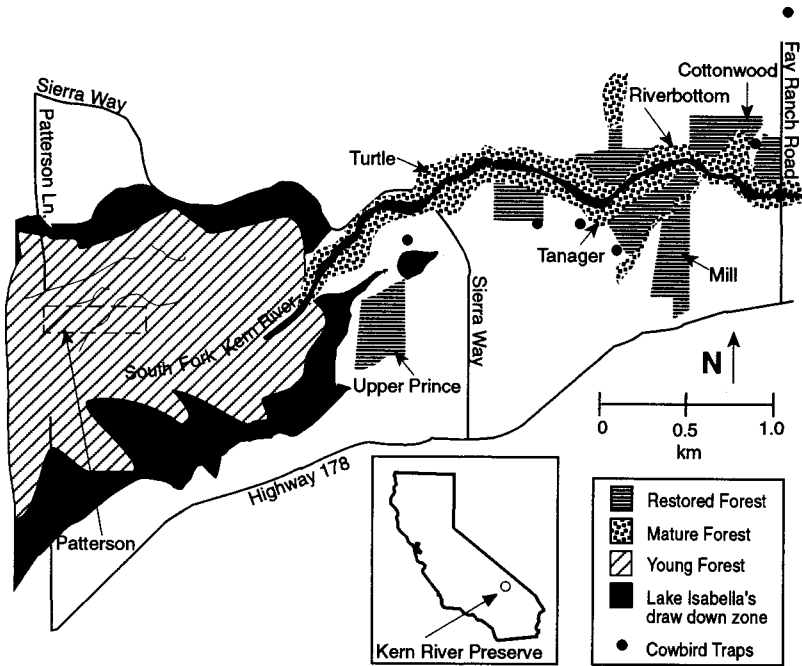


FIGURE 1. Map of study area including the Kern River Preserve and the U.S. Forest Service South Fork Wildlife Area near Weldon, California, showing forest types, and locations of study sites and cowbird traps.

spatial scales (BROAD and LOCAL) influenced sparrow nest-site selection and parasitism.

## METHODS

### STUDY SITES

The study area, located in the South Fork Kern River Valley (elev. 800 m) at the southern end of the Sierra Nevada, California, is willow-cottonwood riparian forest surrounded by uplands of desert scrub and oak woodland (Fig. 1). Although much of the original forest in the region was logged (Fleshman and Kaufman 1984), the remaining riparian forest is one of the most extensive in California. Since 1986, The Nature Conservancy has been restoring riparian habitat at its Kern River Preserve. We examined parasitism in these restored forests and in both mature (not logged) and young (logged but regenerating naturally) forest.

**Restored forest.** Past agricultural use has resulted in substantial habitat degradation of these areas, including not only the loss of forest but the introduction of alien grasses and forbs. Because they are in the secondary flood plain bordering mature forest, such sites are unlikely to experience the flooding which could lead to nat-

ural regeneration in the near future. Restoration efforts to date have consisted of planting native Fremont's cottonwoods (*Populus fremontii*), red willows (*Salix laevigata*), and a small amount of mule fat (*Baccharis salicifolia*). Little re-vegetation of the understory has been attempted to date, and it remains dominated by alien grasses, including *Vulpia octiflora* and *Hordeum* spp., and forbs, such as *Lactuca* sp., *Sonchus* sp., *Cirsium* sp., *Xanthium* sp., and *Cicorium* sp.

In 1993 a single, 14-ha restoration site "Cottonwood," planted in 1991, was studied. Three sites were studied in 1994; Cottonwood, "Mill," a 20 ha site planted in 1992, and "Upper Prince," an 18 ha site planted in 1989. However, because only four nests were found on these additional sites (four on Mill, none on Upper Prince), the 1994 data were pooled prior to analysis.

**Mature forest.** The three mature forest sites (20 ha each) adjacent to the river had historically been grazed, but never deforested. In 1981 all grazing ceased except for winter grazing on "Tanager," and regeneration of trees and understory ensued. These areas, although not pristine, are much less degraded than other nearby areas.

They are dominated by native plant species, and have high density and diversity of bird species (Laymon et al. 1994). Fremont's cottonwoods and red willows are the dominant tree species, and stinging nettle (*Urtica dioica holosericea*), mugwort (*Artemisia douglasiana*), showy goldenrod (*Solidago spectabilis*), and narrow-leaf milkweed (*Asclepias fascicularis*) are common understory species. Interspersed are low marshy areas dominated by bulrush (*Scirpus sp.*) and cattails (*Typha sp.*). A single site, "Riverbottom," was studied in 1993, and three sites, Riverbottom, "Turtle," and Tanager were studied in 1994 (Fig. 1). Data from mature forests were pooled prior to statistical analysis.

*Young forest.* This 16 ha site, "Patterson," located in the U.S. Forest Service's South Fork Wildlife Area, is periodically inundated by a nearby reservoir, Lake Isabella. Riparian forest in this area originally had been cleared for agricultural use. Since 1986, the forest has been regenerating naturally, and consists almost entirely of Goodding's black willows (*Salix gooddingii*), a species which tolerates periodic flooding more than cottonwoods and red willows. Forest understory is dominated by aliens such as rabbit's foot grass (*Polypogon monspeliensis*) and the forbs *Melilotus sp.*, *Cirsium sp.*, and *Rumex sp.*, although thick stands of native stinging nettle and common monkey flower (*Mimulus guttatus*) have become established in some places.

#### VEGETATION SAMPLING

We sampled vegetation in 1994 to compare differences in habitat structure among forest types, and to investigate the effect of habitat structure on nest-site selection and parasitism. Sixteen variables were measured on 93 random plots (35 in mature forest, 29 in restored forest, and 29 in young forest), and an additional three variables were measured only at nests (see below and Table 1). One hundred nests (39 in mature forest, 27 in restored forest, and 34 in young forest) were compared to random plots for analysis of nest-site selection. Comparisons were made between parasitized and nonparasitized nests in order to investigate the effect of habitat structure on nest parasitism. Whether parasitism occurred only was known for a subset of 65 nests (30 parasitized and 35 nonparasitized). Nests that were known to be a second nest of the same pair

were not included in analyses of habitat structure.

Habitat structure was characterized at two spatial scales relative to the nest or random point, that we designated LOCAL and BROAD. Two scales were used because we felt that habitat structure affecting parasitism and nest-site selection might differ depending upon the distance from the nest. LOCAL scale variables were estimated within a maximum of 5 m of the nest or random point, and included foliage cover at vertical intervals of < 1 m, and between 1–2 m and 2–3 m, the number of saplings (< 8 cm dbh), and nest height, substrate, and concealment. The latter three variables relate specifically to nests and were not measured at random points. BROAD scale characteristics were quantified within 11.3 m of the nest or random point (0.04 ha plot). Each plot had 9 sampling points; one at the nest or random point, and one at 5 and 10 m intervals on each of four sampling lines radiating out at right angles to each other. Variables were measured at each sampling point, and the points averaged to produce a single value for a plot. Variables included canopy cover, ground cover, foliage height, lateral cover at vertical intervals of < 1 m, and between 1–2 m and 2–3 m, number of trees (> 8 cm dbh), and percent cover of dominant understory plants such as grasses, forbs, and shrubs, or bare ground. Variables and methods of estimation are summarized in Table 1.

#### NEST MONITORING

Breeding data were collected over two seasons, May–August 1993 and March–August 1994. Active nests were checked every three to four days, which minimized disturbance while allowing us to be certain (within a day or so) of the timing of events such as hatching, parasitism, or failure (Martin and Guepel 1993). Nests in which nestlings survived to the seventh day after hatching were considered successful and, to minimize disturbance, not monitored further.

#### STATISTICAL ANALYSES

Two criteria were used for including nests in analyses of nest parasitism. First, nests were included only if found prior to hatching. Song Sparrows infrequently eject cowbird eggs (Rothstein 1975), and we observed no evidence of ejection. Second, to insure that all the nests in the sample had an equal opportunity to be par-

TABLE 1. Variables relating to habitat structure and methods of estimation. LOCAL scale refers to variables estimated within a maximum of 5 m from the nest or random point. BROAD scale refers to variables estimated within 11.3 m of the nest or random point.

Variable	Method of Estimation
<b>LOCAL Scale</b>	
% Foliage cover at heights of < 1 m, and between 1–2 m, and 2–3 m	Using a 3 m pole marked at 0.1 m intervals, with data recorded at the nest (or center of a random plot), and at 1, 2, and 3 m from the nest along the four sampling lines. If foliage occurred within a radius of 0.1 m of the pole within a 0.1 m segment, we counted one hit. Hits were averaged for each vertical meter.
No. Trees < 8 cm dbh	All saplings within 5 m of the plot center were counted.
Nest height (cm)	Measured from the bottom of the nest to the ground.
Nest substrate	Two species used most in supporting nest.
% Nest concealment	With a 0.25 m radius cloth circle held directly in front of the nest, concealment was the percentage of the circle that was visible 1 m from the nest in four directions around the nest and directly above (Martin 1988).
<b>BROAD Scale</b>	
% Canopy and ground cover	From the number of cells at least half filled with foliage, using an inverted monocular with a 10-cell grid inscribed on a plastic prism (Laymon 1970).
Foliage height	Using a 3 m pole, marked in 0.1 m intervals. If the top of the foliage was above 3 m, we estimated height visually.
% Lateral cover at heights of < 1 m, 0–2 m, and 0–3 m	Using a white canvas cloth (0.5 m wide × 3 m high), divided vertically into three 1-m height sections (< 1 m, 1–2 m, and 2–3 m). Each section was divided into a grid of 50 squares for ease of estimating cover. The cloth was placed at the edge of the plot along each sampling line, and an observer at the center recorded the percentage of squares at least half obscured in each vertical meter (Noon 1981).
No. Trees 8–50 cm, and > 50 cm dbh	Counted all trees within each size class.
% Grass, forb, and shrub cover, and bare ground	Estimated visually, with bare ground defined as any area not covered by either grass, forb, or shrub.

asitized, we included only those that were active until at least the tenth day of incubation.

We used Multivariate Analysis of Variance (MANOVA) (Johnson and Wichern 1988) to compare vegetation structure among forest types. Univariate ANOVAs were used to select variables for inclusion ( $P < 0.15$ ), and Bonferroni tests were used for post-hoc comparisons. Because most of the variables measuring habitat structure were proportions and non-normally distributed, variables were normalized prior to analysis using arcsine transformation (Sokal and Rohlf 1995).

Logistic regression (Hosmer and Lemeshow 1989) was used for analysis of vegetation variables relevant to nest-site selection and parasitism, using STATA 4.0 (StataCorp 1995). Variables were analyzed univariately for inclusion in the initial model ( $P < 0.15$  for inclusion), and logistic regressions were run in a backward stepwise manner, dropping variables from the model

and comparing the constrained model with the previous unconstrained model using a likelihood-ratio test. Analysis was concluded when the most parsimonious significant model was reached. Where interactions between forest type and independent variables were significant, forest types were analyzed separately. Where interactions were not significant, all forest types were included in one analysis, using forest type as a variable. BROAD and LOCAL scale variables were analyzed separately.

## RESULTS

### PARASITISM LEVELS

Parasitism levels were high in the study area in both years. Sixty-three percent of nests were parasitized in 1993, with 92% of nests parasitized in mature forest, and 27% in restored forest. In 1994, 46% of nests were parasitized, 33% in mature forest, 38% in restored forest, and 59%

TABLE 2. Forest type comparisons using random plots.

Variable	Restored (n = 29) Mean ± SD	Mature (n = 35) Mean ± SD	Young (n = 28) Mean ± SD	Univariate ANOVA		MANOVA <sup>a</sup> P	Post-hoc Tests (Bonferroni)		
				F	P		M/R	M/Y	Y/R <sup>b</sup>
<b>LOCAL Scale</b>									
Foliage cover 0–1 m	33.8 ± 9.5	37.8 ± 19.1	44.1 ± 20.0	2.7	ns	—	—	—	—
1–2 m	6.0 ± 4.3	16.1 ± 12.4	11.7 ± 10.5	8.2	***	***	***	ns	ns
2–3 m		9.4 ± 10.3	7.8 ± 7.9	3.6	*	*	*	ns	ns
Trees < 8 cm dbh	8.1 ± 8.4	5.7 ± 11.9	18.4 ± 19.5	8.4	***	***	ns	***	*
<b>BROAD Scale</b>									
Percent canopy cover	21.2 ± 16.0	66.5 ± 26.9	39.7 ± 25.4	29.6	***	***	***	***	*
ground cover	73.2 ± 17.3	33.3 ± 25.3	72.6 ± 23.1	28.0	***	***	***	***	ns
Foliage height	1.4 ± 0.8	6.5 ± 2.9	3.9 ± 3.0	41.4	***	***	***	***	***
Lateral cover 0–1 m	86.8 ± 14.0	92.6 ± 9.5	86.9 ± 16.7	2.0	ns	—	—	—	—
0–2 m	64.6 ± 24.9	71.0 ± 24.7	58.0 ± 29.0	1.6	ns	—	—	—	—
0–3 m	61.8 ± 25.9	54.2 ± 22.7	53.7 ± 29.5	1.1	ns	—	—	—	—
Trees 8–50 cm dbh	0.1 ± 0.4	3.3 ± 3.7	7.3 ± 8.1	26.5	***	***	***	*	***
> 50 cm dbh	0.0 ± 0.0	2.9 ± 2.5	0.0 ± 0.0	4.1	***	***	***	***	ns
Percent grass cover	64.3 ± 28.1	18.9 ± 26.2	30.9 ± 23.9	5.0	***	***	***	ns	***
forb cover	24.6 ± 24.5	37.8 ± 30.9	45.9 ± 24.8	12.2	*	*	ns	ns	*
shrub cover	5.0 ± 4.4	9.3 ± 13.2	2.4 ± 4.2	23.8	***	***	ns	**	ns
bare ground	6.2 ± 7.4	38.6 ± 34.8	18.7 ± 25.2	63.6	***	***	***	**	ns

<sup>a</sup> Wilk's Lambda;  $F_{20,160} = 15.9$ ,  $P < 0.001$ .

<sup>b</sup> M = mature forest, R = restored forest, Y = young forest.

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , ns = not significant; "—" not tested, due to insignificance in preceding analysis.

in young forest. No consistent differences in parasitism levels were found among forest types. However, parasitism levels among forest types were confounded by both a cowbird trapping program which had unequal effects on cowbird numbers in the three forest types (Whitfield and Strong 1995), and by variations among forest types in the density of Song Sparrows and other host species.

#### HABITAT STRUCTURE

*Comparison of forest types.* The three forest types differed markedly in habitat structure at both LOCAL and BROAD scales (Table 2). At the LOCAL scale, restored forest showed lower foliage cover at heights between 1–2 m and 2–3 m than mature forest. Young forest had the greatest number of saplings (trees < 8 cm dbh), probably due to the extensive regeneration after repeated flooding. Forest types also differed at the BROAD scale. Mature forest had greater canopy cover, foliage height, number of large trees (> 50 cm dbh), lower ground cover, and more bare ground than either of the two younger forest types. The lowest canopy cover and foliage height were found in restored forest. Grass cover was highest, and forb cover lowest, in restored forest. No differences in lateral cover were observed among forest types.

*Effect of habitat structure on parasitism.* Two habitat structure variables had significant impacts on parasitism in all three forest types. As there were no significant interactions between habitat variables and forest type (Log likelihood-ratio test,  $P > 0.10$  in all cases), and the same trends were seen in each forest type, the three forest types were pooled in a single analysis, with forest type included as a binary dummy variable.

Foliage cover at heights of 2–3 m (LOCAL; Fig. 2a) and lateral cover at heights of < 1 m (BROAD; Fig. 2b) were associated with parasitism, but had opposite effects. The probability of parasitism increased as foliage cover at heights between 2–3 m increased, and decreased as lateral cover at heights of < 1 m increased. Lateral cover at ground level and foliage cover above the nest-site were uncorrelated in all forest types ( $P > 0.38$  in all cases). Therefore, both of these variables are likely exerting effects on parasitism independently of each other.

*Effect of sparrow nest-site selection.* Song Sparrow nest-site selection influenced the likelihood of parasitism through its effect on both foliage cover at heights between 2–3 m, and lateral cover at a height of < 1 m, the two variables related to nest parasitism. However, selection of nest-sites differed markedly among forest types,

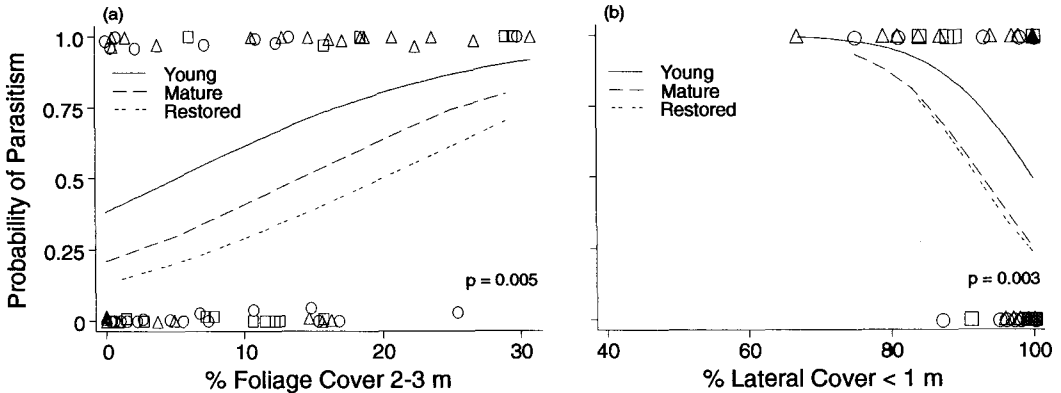


FIGURE 2. Relationship between frequency of Brown-headed Cowbird parasitism of Song Sparrow nests and (a) LOCAL scale habitat structure (estimated coefficient = 0.1,  $\chi^2_2 = 12.9$ ,  $n = 65$ ) and (b) BROAD scale habitat structure (estimated coefficient =  $-0.2$ ,  $\chi^2_2 = 13.9$ ,  $n = 65$ ). Squares represent outcomes of nests in restored forest, circles represent nests in mature forest, and triangles represent nests in young forest. Data points for parasitized nests are shown at probability = 1, for nonparasitized nests at probability = 0. Shading indicates where multiple data points are stacked upon each other. One to two data points are white, 3–5 are gray, and 6–8 are black.

necessitating that logistic regression analysis be carried out separately for each forest type.

Foliage cover at a height of 2–3 m (LOCAL) was associated with nest-site selection (Fig. 3a, b, c), only for sparrows in restored forest. These sparrows preferred to construct nests where there was greater foliage cover, thus greater likelihood of parasitism. At the BROAD scale, increasing lateral cover at < 1 m was associated with increasing probabilities of nest-site selection in both young and restored forests (Fig. 3e, f), potentially leading to reduced levels of parasitism on sparrows in these forest types, but had no effect on nest-site selection in mature forest (Fig. 3d).

Although habitat structure differed markedly among forest types, lateral cover at ground level did not (Table 1). Additionally, lower foliage cover at heights between 2–3 m in restored forest (Table 1) was the only difference among forest types which might have been expected to lead to different levels of parasitism. After nest-site selection, however, there was no difference among nests in different forest types for either lateral cover at ground level (restored  $\bar{x} \pm SD = 96.0 \pm 6.8$ ; mature  $94.6 \pm 10.6$ ; young  $95.3 \pm 7.8$ ;  $F_{2,97} = 0.1$ ,  $P = 0.88$ ) or foliage cover above the nest-site (restored =  $11.8 \pm 9.3$ ; mature  $7.9 \pm 9.1$ , young  $11.2 \pm 9.7$ ;  $F_{2,97} = 1.9$ ,  $P = 0.16$ ), suggesting that parasitism levels among the different forest types were not influenced by differing habitat structure around nests.

## DISCUSSION

The likelihood of nest parasitism depends upon the understory habitat structure of the nest-site, and is influenced by both BROAD and LOCAL scale factors surrounding the nest. At the LOCAL scale, the likelihood of parasitism increased gradually as foliage cover at heights between 2–3 m increased. Only one nest of nine escaped parasitism when foliage cover at this height was greater than 20%. The presence of foliage cover above the nest-site may enhance a cowbird's ability to observe potential hosts by providing perches above the nest-site. Female cowbirds frequently use perches when searching for nests (Norman and Robertson 1975), and studies of parasitism on prairie nesting birds (Johnson and Temple 1990) and Red-wing Blackbirds (Freeman et al. 1990) suggest that the availability of perches may increase parasitism levels.

At the BROAD scale, lateral cover at heights of < 1 m showed a negative association with parasitism, particularly when lateral cover was greater than 90%. When cowbirds locate nests by perching and observing host activities, dense cover may reduce parasitism by concealing activities of the hosts. Dense cover also may make it more difficult for female cowbirds to find nests when actively searching the vegetation for nests (Norman and Robertson 1975). As Song Sparrows typically nested below 1 m, dense cov-

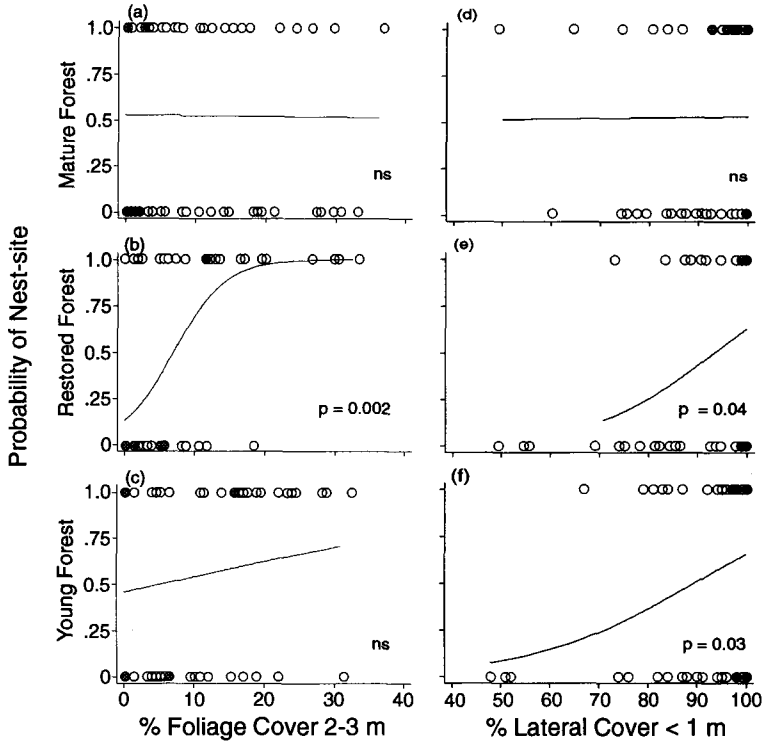


FIGURE 3. Relationship between habitat structure and Song Sparrow nest-site selection, predicted by logistic regression. Circles represent random plots (at probability = 0) and nest plots (at probability = 1). Shading indicates where multiple data points are stacked upon each other. One to two data points are white, 3–10 are gray, and 11–19 are black. Parameter estimates and model  $\chi^2$  for significant relationships; LOCAL (b) Foliage cover in restored forest (estimated coefficient = 1.4,  $\chi^2 = 15.8$ ,  $n = 56$ ); BROAD (e) Lateral cover in restored forest (estimated coefficient = 0.1,  $\chi^2 = 10.0$ ,  $n = 56$ ); (f) Lateral cover in young forest (estimated coefficient = 0.1,  $\chi^2 = 6.9$ ,  $n = 63$ ).

er up to 1 m would help conceal the nest. Additionally, greater cover can increase the time and effort of ground level searches by increasing the number of potential nest sites to be searched (Martin 1993). Thus, in dense vegetation, cowbirds may give up before finding a nest. LOCAL scale variables such as foliage cover at heights of < 1 m and nest concealment had no effect on parasitism levels, suggesting that the main effect of abundant lateral cover at heights of < 1 m is to conceal parental activities in a larger area around the nest. Our results contrast with those of Brittingham and Temple (1996) who found parasitized nests to have dense cover near the ground (0–0.5 m) and to have a more open subcanopy (3–10 m). However, a key difference between their study and ours is that they studied species which typically nest at heights of 1 m or more, whereas we studied a species which nests near the ground.

Habitat type may override microhabitat effects on parasitism levels due to cowbird preferences or other features of the habitat (Burhans 1997). Although we found habitat structure to be related to parasitism, and the three forest types differed greatly in habitat structure, we found no consistent differences in parasitism levels among forest types. One contributing factor may have been the similarity among nests in the different forest types with respect to variables influencing parasitism. This was not true for the Indigo Buntings in Burhans' study. However, confounding factors such as cowbird removal, cowbird densities, and sparrow-to-cowbird ratios, made it impossible to meaningfully examine the effects of forest type in our study.

Whereas the factors influencing parasitism levels are complex, our results suggest that appropriate habitat management has the potential of reducing parasitism levels in some cases. For

example, management efforts that maintain or increase cover at ground level may be a way of reducing parasitism in species that select nest-sites with dense cover at ground level. The effect of increasing vegetation density is of course species dependent and would have no effect on parasitism levels if a host species chose not to nest in denser vegetation. Our findings are particularly relevant to riparian restoration because existing riparian forests typically have degraded understories due to livestock grazing. Grazing alters species composition and decreases herbaceous cover in several plant communities, including riparian ones, leading to reduced avian diversity and reduced nesting densities of some species (Fleischner 1994). Our results suggest that heavy grazing also could reduce nesting success in some species by increasing brood parasitism. Therefore, a possible management strategy to decrease parasitism while improving overall habitat quality would be to manage lands for increased cover.

Future work should address the relationship between parasitism and vegetation structure for other species, particularly those that are threatened and endangered or experience poor reproductive success when parasitized. Optimally, such work would involve exploratory studies followed by experimental manipulation of habitat structure. Because the features of habitat structure associated with parasitism may be related to the nest searching behavior of cowbirds, evaluating cowbird behavior should be helpful in designing such studies. As suggested by differences between our results and those of Brittingham and Temple (1996), habitat features which decrease parasitism in some species may increase parasitism in others. Thus, community-wide studies are essential to fully understand the dynamics of cowbird parasitism.

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