24. Association of Cowbird Parasitism and Vegetative Cover in Territories of Southwestern Willow Flycatchers

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Abstract

We investigated the association of brood parasitism by Brown-headed Cowbirds and vegetation structure in 31 territories of the endangered Southwestern Willow Flycatcher in central California. These flycatchers nest between 1 and 3 m high in riparian forest. We tested whether parasitism varied with concealment on different spatial scales within territories. We predicted that unparasitized flycatchers (N = 13) would have more vegetative cover throughout their territory. We measured vegetation at the nest (nest site), in a 0.04-ha plot around the nest (nest plot), and in a random 0.04-ha plot within the territory (random plot). Cover was characterized using principal component analysis (PCA). Cover at the nest was similar in territories of parasitized and unparasitized birds. Unparasitized flycatchers, however, had more cover in both random and nest plots than parasitized flycatchers. Our results suggest that while all Willow Flycatcher territories had variable densities of understory vegetation and closed canopy, unparasitized flycatchers had larger patches of dense understory. Southwestern Willow Flycatchers may therefore benefit from management activities that increase the density of vegetation below 3 m in height.

Introduction

When female Brown-headed Cowbirds lay their eggs in nests of particular host species, only some nests are parasitized (but see Trine, Chapter 15, this volume). It is therefore of interest to ask, do some nests or hosts share features that affect the likelihood of parasitism? We hypothesize here that concealment from vegetation around the nest and within the territory reduces the likelihood of parasitism.

The effect of vegetative cover on parasitism risk probably depends on cowbirds' nest-searching methods. If cowbirds rely only on visual cues provided by the nest itself, then parasitized nests should have less cover around them than unparasitized nests. It seems likely, however, that cowbirds use both visual and acoustic cues provided by the host to locate nests (Uyehara 1996). Then, parasitism risk could be lower if vegetation concealed activities of the host pair as well as the nest. Masking of such behavioral cues might require dense cover throughout the territory of the nesting pair, not just at the host nest.

We studied a host that nests in riparian forest, the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). In our study area along the South Fork Kern River, 50–80% of all nests have been parasitized in recent years (Harris 1991; Whitfield 1990, Chapter 40 this volume). Nests of different pairs are clustered (Whitfield Chapter 40) with both parasitized and unparasitized nests in each area. The vegetation structure in flycatcher territories is heterogeneous, with open areas containing exposed song perches and dense patches of shrubs, where the flycatchers nest (e.g., Brown 1988, McCabe 1991, Sedgwick and Knopf 1992, Uyehara and Whitfield pers. obs.). In our study area, using univariate analyses, Whitfield (1990) did not find any differences in 15 vegetation variables measured at parasitized and unparasitized nest sites and within 0.04-ha circular plots centered at the nest. We now test the hypothesis that concealment within the whole territory is associated with parasitism events.

Methods

Description of Study Area

Our study site was located along the South Fork Kern River in central California (35° 40' N, 118° 20' W, elevation 762–805 m). The study area lies in a broad, braided-river valley that drains the southern Sierra Nevada. The riparian forest along the river is bordered by pastures and cultivated fields. The forest is narrow, with the interior no farther than 200 m from an edge or opening, and is dominated by red willow (*Salix laevigata*), black willow (*S. gooddingii*) and Fremont cottonwood (*Populus fremontii*). The understory includes young willow in thickets, mule fat (*Baccharis viminea*), and hoary nettle (*Urtica dioica holosericea*). Open areas of grass or freshwater marsh are interspersed throughout the forest. More detailed descriptions are found in Harris et al. (1987:28–29), Whitfield (1990 and Chapter 40), Harris (1991), and Uyehara and Narins (1995).

At our study site, Willow Flycatchers begin arriving in early May. By late May, territorial boundaries are stable and discrete, as seen in other Willow Flycatcher populations (e.g., Sedgwick and Knopf 1988). A pair's territory was defined as the area enclosed by perches used by the nesting pair. Pairs were determined by nesting phenology, vocalizations during nest searches and checks, observed flight patterns, and locations of banded birds (ca. 25% of adults in the population).

Brown-headed Cowbirds arrived in large numbers from mid- to late April. In 1989 and 1990, cowbirds were abundant (pers. obs.). In 1991, 60 15-min point counts separated by 200 m averaged 1.55 female cowbirds/point and 2.67 male cowbirds/point from May through June.

From late May through July, 1989–1990, we monitored Willow Flycatcher nests. After nests were no longer in use, we measured the vegetation. The delay in measuring vegetation probably had only small effects on the data because (1) trees and forbs changed little from June through August, and (2) delays were short and equal for parasitized and unparasitized pairs. Grass height may have changed over time but did so only below 1 m.

We took three sets of vegetation measurements in each territory. We measured habitat variables at the nest site, in a 0.04-ha circular nest plot (radius = 11.3 m) around the nest, and in a 0.04-ha random plot. Random plots were selected by blindly picking numbers and directions from a bag. Random plots were 23–50 m from the nest but within the territory of the pair.

Measurements taken at the nest site were percentage of nest cover, nest height, distance to top of canopy from the nest, and percentage of canopy cover. The seven variables measured in nest plots were (1) canopy height, (2) percentage of ground cover, (3) percentage of canopy cover, and (4–7) percentage of foliage cover at height intervals of 0–1 m, 1–2 m, 2–3 m, and 3–4. Measurements on random plots were identical to those on the nest plot. Our vegetation sampling methods are modified from James and Shugart (1970) and Noon (1981).

Percentage of cover at the nest site was estimated using a 1- x 0.5-m grid marked with 50 0.1-m cells. The grid was positioned behind the nest, centered on it, and observed from 5 m in four cardinal directions. The percentage of nest cover was estimated as 2x the number of cells that were at least 50% concealed by vegetation.

All height measurements were estimated using a 4-m pole marked at 10-cm intervals. Ground and canopy cover were measured by peering through the objective lens of a 7x, 6.2° monocular with a 10-cell grid attached 7.6 cm from the eyepiece (details in Laymon 1988). Percentage of cover was estimated as 10x the number of cells in which 50% or more of the cell was obscured by vegetation. For nest plots and random plots, eight measurements were taken, at 5 m and 11 m from the plot center in the four cardinal directions.

Percentage of foliage cover was measured using a 1-x-0.5-m grid subdivided into 50 10-cm cells. We calculated the estimate as 10x the number of cells in which 50% or more of the cell was obscured by vegetation when viewed from the center to the edge of the circular plot at the appropriate heights.

Data Analysis

Because vegetation features were correlated within plots, scores obtained by principal component analysis (PCA) were used to describe vegetation on territories. PCA reduced the vegetation variables to independent axes, with a few variables contributing significantly to each.

Each territory received one score for each axis. Scores for each axis were normally distributed with a mean close to zero. A score of 0 indicated that a territory had average values, especially for the vegetation variables that loaded heavily on the axis. An extreme score indicated that the territory had extreme values for the most heavily weighted variables. We used only the first two axes, noting which variables had component loadings with values greater than 0.5. Territory scores were divided into parasitized and unparasitized groups and tested for differences in cover by a Mann-Whitney U-test.

Results

Data from 17 variables for 19 parasitized territories and 14 unparasitized territories were used for the PCA (Table 24.1). The first two axes explained 30.05% and 18.13%, respectively, of the total variance in the data. The component loadings for the first axis indicated that high-scoring territories had dense understory vegetation (1–4 m) and relatively tall and continuous canopy in the random plot (Table 24.2, Figure 24.1). Canopy cover values were also high on the nest plot (Table 24.2). The mean score of unparasitized territories (0.24) was higher than that of parasitized territories (-0.16), but not significantly so (Mann-Whitney U-test, U = 88.5, P = .13, one-tailed).

Loadings for the second axis indicated that high-scoring territories had dense understory vegetation at the nest site itself, at 0–3 m height within 0.04 ha of the nest, and in the nest plot (Table 24.2, Figure 24.1). The mean score for unparasitized nests was significantly higher than scores for

Table 24.1. Mean Vegetation Measurements for 19 Parasitized (P) and 14 Unparasitized (NP) Territories from 1989 and 1990

Parameter	P/NP	Nest Site	Nest Plot	Random Plot
Nest height	NP	2.23 (0.32)	–	–
(m)	P	2.21 (0.29)	–	–
Canopy height	NP	7.11 (0.88)*	4.79 (0.57)	5.04 (0.83)
(m)	P	6.76 (0.39)	5.16 (0.31)	3.45 (0.45)
Ground cover	NP	–	28.29 (11.34)*	–
(%)	P	–	47.22 (9.52)*	–
Canopy cover	NP	93.67 (5.31)	76.63 (4.91)	63.22 (8.40)
(%)	P	94.53 (2.22)	68.40 (4.22)	49.15 (5.94)
Foliage cover	NP	92.27 (4.41)	–	–
(%)	P	89.37 (2.26)	–	–
0–1 m	NP	–	97.46 (1.59)	86.16 (3.92)
	P	–	96.12 (2.36)	84.84 (3.75)
1–2 m	NP	–	95.92 (2.42)	83.48 (4.50)
	P	–	92.26 (2.08)	68.31 (5.24)
2–3 m	NP	–	92.79 (2.56)	74.81 (6.63)
	P	–	86.53 (2.85)	67.06 (5.68)
3–4 m	NP	–	91.34 (3.09)	72.51 (6.96)
	P	–	88.23 (2.96)	63.46 (6.94)

Note: Measurements were taken at the nest (Nest Site), within a 0.04-ha plot centered around the nest (Nest Plot) and in a randomly selected 0.04-ha plot within the territory of the pair (Random Plot). Values within parentheses are one SE.
*Sample size reduced by 1, $N = 18$ for parasitized plots and $N = 13$ for unparasitized plots.

Table 24.2. Habitat Measurements of Axes 1 and 2 for Which Eigenvector Values were Greater than 0.5

Type of Plot	Habitat Variable	Value
Axis 1		
Random plot	% foliage cover, 2–3 m	0.882
Random plot	% canopy cover	0.861
Random plot	% foliage cover, 3–4 m	0.836
Random plot	% foliage cover, 1–2 m	0.818
Random plot	Canopy height	0.743
Nest plot	% canopy cover	0.616
Axis 2		
Nest plot	% foliage cover, 0–1 m	0.741
Nest plot	% foliage cover, 1–2 m	0.703
Nest plot	% foliage cover, 2–3 m	0.688
Nest site	% foliage cover, at nest	0.648

Note: Habitat measurements that had component loadings less than 0.5 are not listed.

parasitized nests, 0.21 and -0.15, respectively ($U = 74.0$, $P = .04$, one-tailed).

Discussion

Southwestern Willow Flycatchers differed in the amounts of cover at different spatial scales within their territories. Territories varied most in the amount of cover at randomly selected sites within the territory, but cover on random plots did not differ greatly between territories of parasitized and unparasitized pairs. Parasitized and unparasitized territories did, however, differ in cover provided by understory vegetation at and near the nest (nest site and nest plot). Willow Flycatchers typically placed nests in denser vegetation than was found near the nest or on random plots. Nests were usually 1–3 m high (e.g., Whitfield 1990, Harris 1991, McCabe 1991) and, again, in denser vegetation than was available at this height on random plots in the territory. Dense vegetation at the nest site is typical of Willow Flycatchers (e.g., Brown 1988, McCabe 1991, Sedgwick and Knopf 1992).

Well-concealed nests alone did not reduce parasitism for Willow Flycatchers (Whitfield 1990 and Chapter 40). Song Sparrows (*Melospiza melodia*) on Mandarte Island also showed no correspondence between nest concealment and parasitism (Smith 1981). Yellow Warblers (*Dendroica petechia*) breeding in an open burned area did not suffer increased parasitism compared to a control site or preburn year (Howe and Knopf, Chapter 23, this volume). Taken together, these studies suggest that vegetation characteristics at the nest site itself are unreliable predictors of parasitism (but see Sealy et al. 1995 for an alternative hypothesis).

Parasitism frequency was associated with vegetation features on a larger scale than at the nest site. The vegetation characteristics in the rest of the territory differ from those at the nest site (Sedgwick and Knopf 1992, this study). This variation in cover was associated with parasitism in Southwestern Willow Flycatchers. Unparasitized nests tended to be in territories with more cover in both the random and nest plots than in parasitized territories, although the difference in scores was significant only at the scale of the nest plot (Axis 2). In contrast, parasitized flycatchers occupied territories that had more heterogeneous vegetation with dense cover at the nest site, but less cover overall in the territory. Therefore, to avoid being parasitized in areas with high numbers of cowbirds, Willow Flycatchers may need to nest in territories with large patches of thick, dense understory merging with closed canopies, as indicated by the component loadings of Axis 2.

Few studies have associated territorial forest structure with parasitism frequencies. Our study indicates that in a riparian forest with many edges or openings, cover is associated with parasitism. Wolf (1987) categorized habitats as open or closed canopy and found significant differences in the frequencies of parasitism in Dark-eyed Juncos (*Junco hyemalis*) in these habitats in one of two years. Winslow et al. (Chapter 34, this volume) reported that nests of some species near forest openings had higher parasitism rates than interior nests. Woodworth (1995) found no significant edge effect in parasitism events of Shiny Cowbirds in an open-canopy forest in Puerto Rico.

Thus, lack of canopy cover does not always correlate with higher frequencies of parasitism. Mixed results might occur if cowbirds predominantly search for and parasitize nests below the canopy (Norman and Robertson 1975, Wiley 1988, Briskie et al. 1990, Hahn and Hatfield Chapter 13; but see Robinson et al. Chapter 33) or if canopy cover is correlated with other factors affecting parasitism.

The association of parasitism with vegetation on territories may be due to the effect of dense vegetation on the searching behavior of female cowbirds. Cowbirds use elevated perches from which they scan for potential hosts (e.g., Friedmann 1963, Norman and Robertson 1975, Payne 1973, Darley 1983, Wiley 1988, Uyehara 1996; but see Freeman et al. 1990 regarding available perches). Female cowbirds probably use visual and acoustic cues from hosts to find nest sites (Hann 1941; Robertson and Norman 1976, 1977; Smith 1981; Smith et al. 1984; Wiley 1988; Uyehara and Narins 1995; Uyehara 1996). For example, Wiley

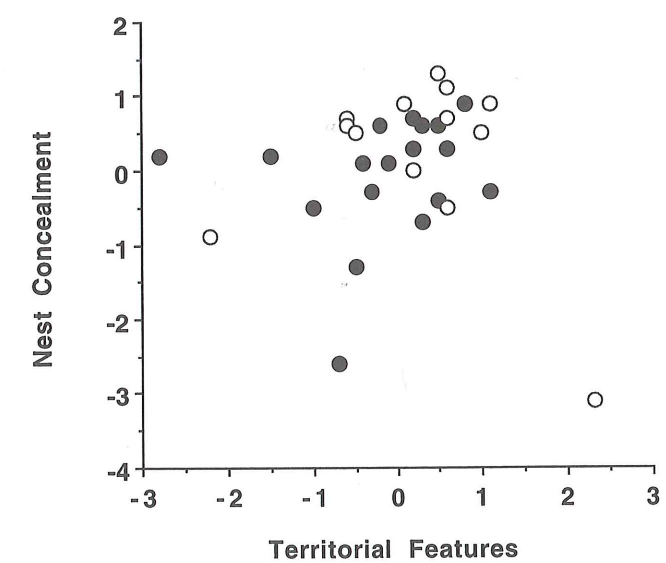

Figure 24.1. Scores of parasitized (solid circles) and unparasitized (open circles) territories of Southwestern Willow Flycatchers derived from principal component analysis. For Axis 1 (territorial features), high positive scores indicated more dense vegetation 1–4 m high and taller forest with greater canopy cover in random plots. For Axis 2, high scores indicated more dense vegetation 0–3 m high and more foliage cover in the nest plot. Scores close to 0 indicate average vegetation cover for the territory.

(1988) observed Shiny Cowbirds flying to sites where hosts had been building nests or actively defending territories. It is therefore likely that dense vegetation will impede their ability to observe host behavior and to discover nest sites from a distance.

Searching cowbirds have been observed beating shrubs (Norman and Robertson 1975, Wiley 1988) and walking in forests while looking up at passing birds (Norman and Robertson 1975; Hahn and Hatfield, Chapter 13, this volume). Because of the presence of water and dense vegetation below 4 m in height in our study area, cowbirds would have found it difficult to walk in this habitat.

In Song Sparrows, older birds are more likely to be parasitized because they are more aggressive toward cowbirds (Smith and Arcese 1994). If both aggressive behavior and habitat use are correlated with age in flycatchers, an alternative interpretation of our results is that parasitized birds were older, more aggressive, and occupied areas with more heterogeneous vegetation. In support of this idea, Willow Flycatchers at seven parasitized nests were noisier than flycatchers at six unparasitized nests (Uyehara and Narins 1995) at Kern River Preserves 1 and 2 (Whitfield, Chapter 40, this volume). Unfortunately, we have few data on the age structure in our population that could be used to compare the habitat use and behavior of older and yearling flycatchers.

Management Implications

Southwestern Willow Flycatchers nested in shrubs or understory in riparian forest that provided relatively high amounts of cover (Brown 1988, Whitfield 1990, this study, M. Sogge pers. comm.). The riparian forest in our study area is generally narrow and linear with many openings. In this area, unparasitized pairs nested in territories with larger patches of dense understory and contiguous canopy, although there were still many forest openings.

Our results suggest that forest management to enhance dense understory and canopy cover may benefit Southwestern Willow Flycatchers. However, we did not address whether similar benefits would prevail in unfragmented forests or if enhancing shrub and canopy cover might adversely affect other species nesting in riparian habitats. These issues also need to be considered before action is taken.

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