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NEST DEFENSE BY WILLOW FLYCATCHERS TO BROOD-PARASITIC INTRUDERS[1]

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Abstract. Nest defense behaviors are defined as counteradaptations to brood parasitism if the defensive behaviors are (1) beneficial and (2) specific to brood parasites. Specificity implies recognition of parasites and host responses tailored to brood parasite intrusions. We investigated the adaptive value and specificity of Willow Flycatcher (*Empidonax traillii*) responses to simulated and live intrusions of Brown-headed Cowbirds (*Molothrus ater*). We hypothesized that flycatchers which were quieter near their nests were less likely to be parasitized. Parasitism was associated with noisier flycatcher pairs, suggesting that inconspicuous behavior was adaptive for this heavily parasitized population.

The flycatchers' responses to cowbird intrusions differed depending on the context of intrusions. Flycatchers chased female cowbirds near the nest (<2 m) but not cowbirds further from the nest nor other species which approached to within 2 m. Preincubation behavior (sitting in the nest) was observed in 42% of flycatcher nests during live and simulated cowbird intrusions. We tested whether flycatchers responded adaptively (quietly) to playbacks of female cowbird vocalizations distant (5 m) from the nest. In our first experiment, flycatchers were quieter in response to calls of a brood-parasite than they were to a playback of a nonparasitic species (Rufous-sided Towhee). In a second experiment, parasitized and unparasitized flycatchers did not differ in their response to female cowbird calls. Taken together, our results suggest that this population of Willow Flycatchers differentially recognized female cowbirds and differentially responded to female cowbirds, depending on the cowbird's distance from the nest. This response did not appear to differ with the experience of parasitism.

Key words: Counteradaptations; Willow Flycatchers; Brown-headed Cowbirds; host defense; brood parasite; Empidonax traillii; Molothrus ater.

INTRODUCTION

Counteradaptations evolve as beneficial responses to a trait of another species, e.g., a brood parasite (Dawkins and Krebs 1979, Davies and de L. Brooke 1988, Rothstein 1990). Brood parasites such as the Brown-headed Cowbird (*Molothrus ater*) lay eggs in the nests of potential host species. Even when birds accept cowbird eggs, hosts may have counteradaptations that minimize the impact of cowbird actions. Because female cowbirds find host nests and, also, remove host eggs (e.g., Scott et al. 1992), hosts could respond to cowbirds as nest intruders (Rothstein 1975), nest predators, or egg-layers.

Host behaviors which prevented nest discovery by the cowbird would be most adaptive. If cowbirds used host behavior as a nest finding cue (Robertson and Norman 1976, 1977; Smith 1981; Smith et al. 1984; Wiley 1988; Uyehara and Narins, unpubl. manuscript), counteradaptations might consist of inconspicuous behaviors, e.g., being quiet around the nest. The adaptive value of inconspicuous behaviors may be dependent on the parasite's distance from the nest (McLean 1987, Moksnes et al. 1990, Duckworth 1990, McLean and Rhodes 1991). Nest guarding or preincubation behavior (sitting in the nest) has been reported for a small host species in response to cowbird presence (Burgham and Picman 1989, Hobson and Sealy 1989). However, if female cowbirds are close to the nest, a host pair might deter intruding brood parasites or egg predation by utilizing conspicuous, aggressive nest defense (Slack 1976, Robertson and Norman 1977, Folkers and Lowther 1985, Davies and Brooke 1988, Graham 1988, Briskie and Sealy 1989, Moksnes and Roskaft 1989, Neudorf and Sealy 1992). This behavior would be a counteradaptation if it was specifically directed to female cowbird intruders and if the cowbird left the area without locating the nest or if egg predation were prevented.

Willow Flycatchers (*Empidonax traillii*) are a small (12 g) host. Because these birds are green and nest in dense vegetation, they tend to be inconspicuous except when the flycatchers are vocal. Both male and female Willow Flycatchers

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sing (Seutin 1987). In addition, flycatchers have several calls used in response to intruders or to the presence of the mate (McCabe 1991 and refs therein; pers observ.). In playback studies of northern populations, Willow Flycatchers responded noisily and aggressively (Stein 1963, Barlow and McGillivray 1983, Prescott 1987, McCabe 1991).

The population of Willow Flycatchers in the South Fork Kern River Valley in southern California has been heavily parasitized with a subsequent reduction in nesting success (Harris 1991, Whitfield 1990, Whitfield, in press). We asked whether this southern population of Willow Flycatchers had developed behavioral defenses to cowbirds in the 80 years since cowbirds invaded this valley (Laymon 1987).

If noisy behavior near the nest is maladaptive, then we would predict that parasitized flycatchers would be noisier than nonparasitized pairs. Second, we observed the incidence of aggressive defense (chasing) or inconspicuous behavior (sitting in the nest) against intruders at different distances from the nest. Third, we compared the response of Willow Flycatchers to female cowbird or Rufuous-sided Towhee *(Pipilo erythrophthalmus)* vocalizations which were presented distant (≥ 5 m) from the nest. We predicted that Willow Flycatchers would become quieter in response to a cowbird playback. Fourth, we compared the responses of parasitized and unparasitized flycatchers to female cowbird vocalizations.

MATERIALS AND METHODS

SITE DESCRIPTION

The study site is a flat, braided-river valley on the southern edge of the Sierra Nevada Mountains (circa 35°38′N, 118°15′W, elev 822 m). It consists of a narrow riparian forest along the South Fork Kern River, and is bordered by pastures, either currently in use or abandoned in the last 15 years (Harris et al. 1987). Major riparian tree species are willows (*Salix* spp.) and Fremont cottonwood (*Populus fremontii*). Where present, the understory generally consists of young willow, mulefat (*Baccharis salicifolia*) or hoary nettle (*Urtica dioica*). Understory vegetation can form dense thickets.

GENERAL METHODS

We observed Willow Flycatchers during egg-laying and early incubation. If flycatchers are parasitized during these stages, nesting success is low (Whitfield 1990, pers comm.). To observe birds, we sat under and in dense vegetative cover, 2–8 m from the nest (1990) or >5 m from the nest and speaker (1991 and 1992). Minimum observation periods at each nest were 70 min (1990), 130 min (1991), and 60 min (1992).

For all observation periods, the number and types of vocalizations of Willow Flycatcher and cowbirds were recorded. Locations of Willow Flycatchers, cowbirds and other intruder species were recorded as distance from the nest (in nest, 0–2 m, 2–10 m). Willow Flycatchers or other birds perched or vocalizing were also noted whenever possible. Chasing by flycatchers was recorded along with the intruder identity and location of the chase. The incidence of preincubation behavior was recorded for egg-laying pairs.

Comparison of flycatcher vocalizations at parasitized and unparasitized nests. Two-hour observation periods at nests of Willow Flycatchers were conducted from 22 June to 26 July 1991, between 07:00 and 10:00. Nests were categorized as parasitized if a cowbird egg was present by the sixth day of incubation.

For five pairs, we monitored vocalizations for two or more mornings. Because the median number of vocalizations was similar between days for these pairs (Pearson correlation coefficient, $r = 0.88$), eight nests were monitored once. One other nest was determined to be abandoned.

Observation periods for each nest were divided into 60 2-min periods. Distributions of vocalizations were skewed so we identified the median number of vocalizations per 2-min period, then calculated the median vocalization rate per minute as a baseline rate. For nests observed twice, the mean of the baseline from the two periods was used in the data analyses.

Construction of playback tapes. The playback stimuli for each species consisted of vocalizations from a number of individuals on the same tape. For the towhee playback, the stimulus tape consisted of a series of three songs from Bird Songs of California (Sander 1989) and songs from three individuals recorded on different days in Kern County in 1989. The tape averaged 6.6 songs/min with average duration/song of 0.91 sec. The cowbird stimulus tape was composed of seven chatter exemplars (6.9 chatter/min with average duration of 1.14 sec) from three female cowbirds recorded in Mono County, CA, by S. Rothstein.

Playback Experiment 1. From 23 June–28 July 1990, nine flycatcher nests were tested on separate days in playback experiments of female cowbird 'chatter' and a control species (Rufous-sided Towhee). Experimental nests were separated by >40 m. Playback sessions were conducted during the hours of 08:00–10:15. We used a Sony TCD-5M recorder, Cal-Rad preamplifier and Mineroff speaker to broadcast playbacks at a height of 1.15 m and horizontal distance of 5 m from the main stem(s) holding the nest. Equipment was set up a minimum of 20 min before observation periods began.

Peak sound pressure levels were measured by placing a sound level meter (GenRad 1982) at eight nest sites, after nestlings had fledged. The speaker was located at 5 m from the nest, as it was during playback experiments. The averaged peak levels for all playback stimuli measured for towhee and cowbird vocalizations were 80.6 dB SPL and 84.7 dB SPL, respectively.

Each session at a nest started with a preplayback observation period. After this initial period, we randomly selected and played either the towhee stimulus or female cowbird "chatter," followed by a 10-min quiet period. The alternate stimulus was then presented. Stimuli were broadcast for 10 min so that live intruders would be attracted to the area and the response of the flycatchers could then be recorded. However, because variable numbers of intruders were attracted to the speaker, the conditions across playback trials were not comparable except for the first two minutes of each playback. No female cowbird or towhee was detected within 5 m from the nest for the first two minutes of all playbacks. Therefore, the initial conditions were comparable between trials.

We investigated whether flycatchers were quieter during the initial period of cowbird or towhee playbacks when compared to their baseline vocalization for that particular morning. Flycatcher responses were calculated as the difference in vocalization number during the first 2-min of a playback and the pair's baseline level. Baseline rates for a pair of flycatchers were calculated as the mean of the number of vocalizations of three 2-min observation periods: (1) before the first playback, (2) eight minutes after the first playback and before the second playback, and (3) eight minutes after the second playback.

Playback Experiment 2. From 27 June–24 July 1991, female cowbird 'chatter' was played at 12 nests on different days at the end of a 2-hr observation period. All playbacks were separated by a minimum of 30 m. Equipment was set up ≥2 hr prior to playback with a Mineroff speaker placed 5 m from the stem(s) holding the nest at 1.15 m height. The mean peak level at 5 m for female cowbird 'chatter' was 70.1 dB SPL at nine nest sites.

Flycatcher response was calculated as the difference in the number of vocalizations during the 2-min of playback and their baseline rate (the median of vocalization number during the previous 60 2-min observation periods). Each nest was tested once.

TABLE 1. Incidence of Willow Flycatchers chasing intruders at distances of less than 2 m from the nest and at 2–10 m from the nest. Nests are categorized as parasitized (Par) or not parasitized (NP).

Year	Par/NP	Female Cowbird <2 m	Female Cowbird 2–10 m	Noncowbird <2 m
1990	Par	2/2	0/2	1/6
	NP	3/3	0/2	3/6
1991	Par	2/2	2/6	5/12
	NP	1/1	1/6	4/8
1992	Par	2/4	No data	0/4
Total		10/12	3/16	13/36

RESULTS

RESPONSE TO LIVE INTRUDERS

Both parasitized and unparasitized flycatchers chased female cowbirds which approached within 2 m of the nest (Table 1). Intruder species were usually Song Sparrows (*Melospiza melodia*), but goldfinches, a male Red-winged Blackbird (*Agelaius phoeniceus*), wrens, Common Yellowthroats (*Geothlypis trichas*), male cowbirds, hummingbirds, and Willow Flycatchers also passed within 2 m of the nest.

For a conservative statistical analysis, the behavior of Willow Flycatchers at each nest was counted once for a particular category. For example, if a flycatcher did not chase four noncowbird intruders but chased a fifth noncowbird intruder, the flycatcher was counted once as chasing noncowbird intruders. To be categorized as a nonaggressive flycatcher, the flycatcher was not observed chasing any noncowbird intruders.

At eight nests where female cowbirds were near the nest (<2 m), flycatchers at six nests were observed chasing nearby cowbirds one or more times. Of 16 nests where female cowbirds were distant from the nest (>2 m), flycatchers chased distant female cowbirds from three nests. The

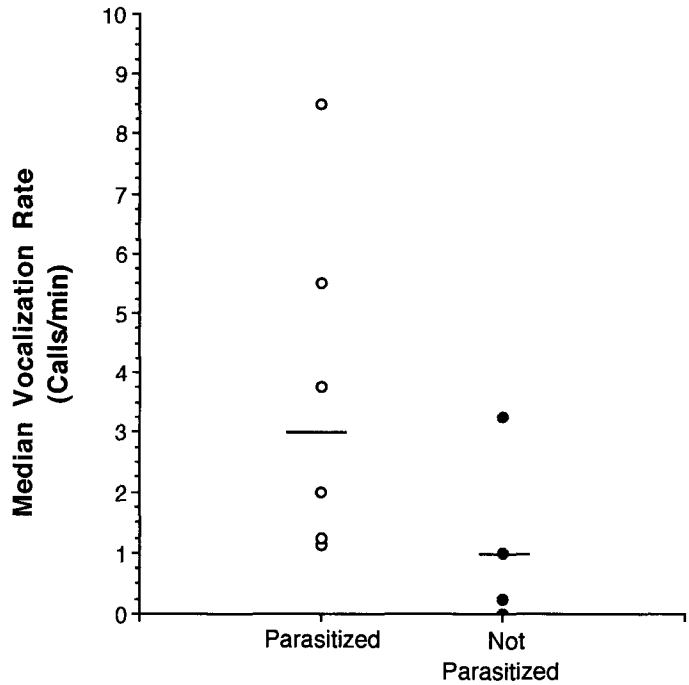

FIGURE 1. Median number of vocalization rates produced by parasitized (n = 7) and unparasitized (n = 6) pairs of Willow Flycatchers. Two parasitized pairs had median vocalization rates of 1.25. Three of the unparasitized pairs had median vocalization rates of 1.00 call/min. Bars represent the median of all vocalization rates by parasitized or unparasitized pairs.

proportion of nearby cowbirds is significantly greater than the proportion of distant cowbirds that were chased (Fisher's Exact Test, $P < 0.010$). At eight of 24 nests, noncowbird intruders were chased at least once when they were close to the nests. Noncowbird species were chased significantly less often than female cowbirds (Fisher's Exact Test, $P < 0.020$).

PREINCUBATION BEHAVIOR

Preincubation behavior (sitting in the nest) can only be observed in egg-laying pairs. During simulated and live female cowbird intrusions at 12 nests, flycatchers exhibited preincubation behavior at five nests. In 1992, a flycatcher sat in the nest when only a sparrow was detected in the area and not during a "chatter" playback.

Comparison of flycatcher vocalizations at parasitized and unparasitized nests. The number and types of vocalizations were recorded at 13 active nests. The median vocalization rate at seven parasitized nests, 2.87 calls/min, was higher than at six unparasitized nests, 1.00 call/min (Fig. 1; Mann-Whitney U test, $U = 38$, $P = 0.014$).

Playback Experiment 1. Eight pairs of flycatchers were quieter during the female cowbird 'chatter' playback than they were when no stimulus was presented or during the towhee playback (Fig 2). Because the same flycatchers were tested under different treatments, the data were not independent. We therefore compared the behavior of flycatchers at each nest during playbacks with their baseline vocalization rate. The Willow Flycatchers became quieter in response to cowbird chatter (Wilcoxon signed-ranks test, $Z = -1.693$, $P = 0.045$). Flycatchers did not respond to towhee playbacks (Wilcoxon signed-ranks test, $Z = -0.704$, $P = 0.482$).

Playback Experiment 2. At three parasitized nests, female cowbirds approached the speaker during the playback, thus changing the conditions of the experiment. At another four parasitized nests and five unparasitized nests, flycatchers' response to the 'chatter' playback did not differ (Fig. 3; Mann Whitney U test, $U = 12.0$, ns).

Summarizing, noisy Willow Flycatchers were more likely to be parasitized than quieter fly-

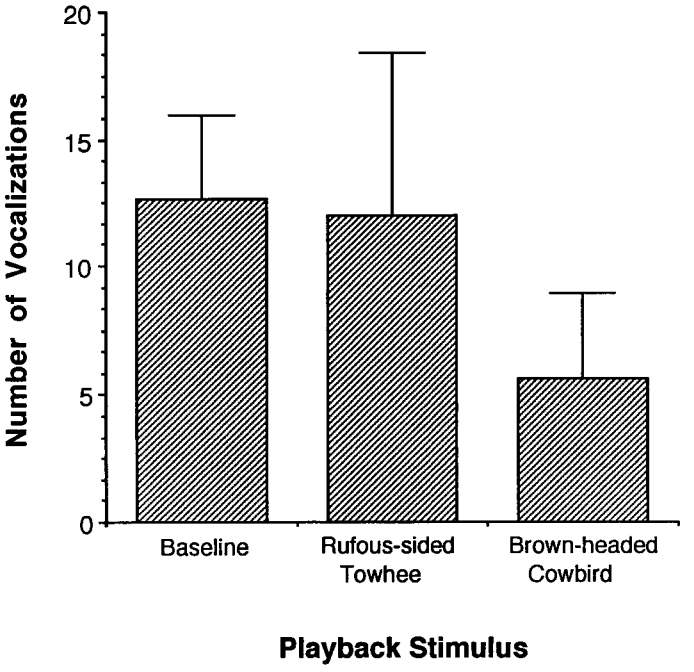

FIGURE 2. The mean number of vocalizations by Willow Flycatchers during nonplayback periods and during playbacks of Rufous-sided Towhee and female cowbird 'chatter'. Bars represent one standard error.

catchers. Willow Flycatchers chased nearby female cowbirds (<2 m) significantly more often than distant female cowbirds (>2 m). Willow Flycatchers responded quietly to female cowbird calls 5 m from the nest, but towhee playbacks did not affect their vocalization rates. Parasitized and unparasitized flycatchers did not differ in their response to female cowbird playbacks although sample sizes were small.

DISCUSSION

During morning hours, female cowbirds search for nests and remove eggs from hosts' nests (e.g., Scott et al. 1992). Thus, during morning hours, counteradaptations of hosts would either prevent egg predation or nest-site discovery. Willow Flycatchers appear to have several defensive strategies but, which strategy is chosen may depend on the context of intruder identity and location.

If host behavior such as aggression (Robertson and Norman 1977, Smith et al. 1984) or host vocalizations are used as nest-finding cues by female cowbirds, then we predicted that nests of noisier pairs would be parasitized. Our results from 1991 suggest that vocalization rates are associated with parasitism. In 1991, 80% of the nests built by 27 pairs were parasitized (Whitfield, pers comm.). Yet, those nests of flycatchers with lower vocalization rates were not parasitized. This suggests there has been selection for more cryptic, less vocal behavior in this population. To our knowledge, this is the first case where quietness has been found to be advantageous around brood parasites.

An alternative interpretation would be that parasitized Willow Flycatchers are noisy because they had more female cowbirds or a particularly persistent cowbird in their territories. However, this seems unlikely. The morning range of female cowbirds in southern California is much larger than Willow Flycatcher territories (e.g., Rothstein et al. 1984), yet parasitized and unparasitized flycatcher nests were interdigitated. In 1991, the cowbird density was uniform in areas where we observed flycatchers (Whitfield, in press). In addition, female cowbirds were observed near parasitized and unparasitized nests (Table 1). Thus, the presence of cowbirds in the flycatchers' territories does not account for the difference in parasitism.

In southern California, cowbirds invaded approximately 70 years ago (Laymon 1987). Thus, if quietness is a beneficial trait in populations with high parasitism rates, it would be interesting

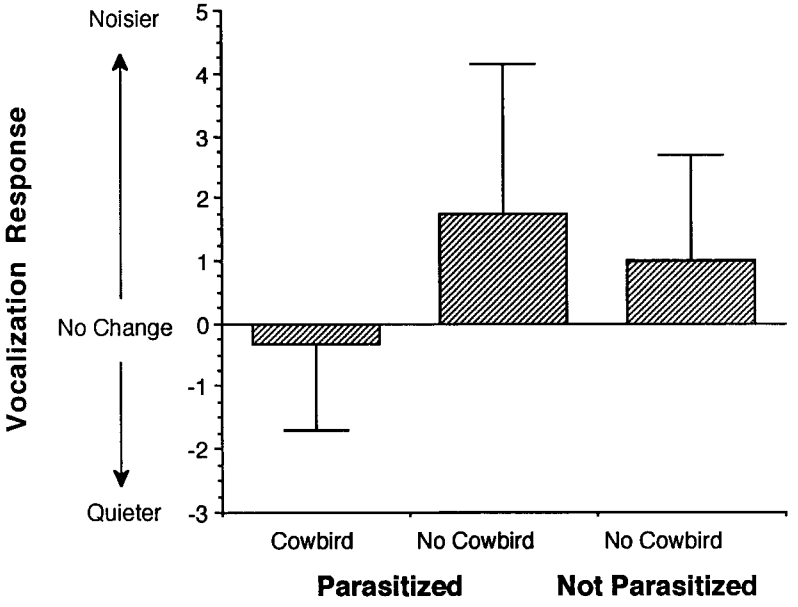

FIGURE 3. The response of Willow Flycatchers to playbacks of female cowbird vocalizations at parasitized (n = 4) and unparasitized (n = 5) nests when no cowbird was present. Vocalization response is defined as the number of vocalizations during the playback minus the median rate of vocalizations in the previous two hours. At another three parasitized nests, female cowbirds approached changing the experimental conditions.

to compare the vocal behavior of other populations of Willow Flycatchers at sites with lower cowbird densities. We would predict that these other populations would have higher vocalization rates near their nests.

Being quiet around nests is adaptive for many reasons. To demonstrate that Willow Flycatchers have or are evolving antiparasitic defenses, responses by flycatchers should be specific to activities of female cowbirds as well as adaptive (Rothstein 1990, Neudorf and Sealy 1992). Our results are equivocal regarding this second requirement of counteradaptations.

Our hypothesis was that flycatcher response to female cowbirds would vary depending on context. We tested flycatchers during the nesting stages when parasitism would reduce their nesting success. A cowbird near the nest increases the egg predation threat whereas a distant cowbird or another species near the nest may represent no threat. Therefore, flycatchers might benefit from preferentially chasing female cowbirds that were close to their nest. Our results support the idea that Willow Flycatchers chase near female cowbirds but not distant cowbirds or near intruders of other species. This suggests that Willow Flycatchers specifically respond to female cowbirds. Other host species also respond specifically and aggressively to brood parasites near the nest (Clark and Robertson 1981, Smith et al. 1984, Burgham and Picman 1989, McLean 1987, Moksnes et al. 1990, Duckworth 1990, McLean and Rhodes 1991, Briskie et al. 1992, Neudorf and Sealy 1992). However, our results do not distinguish whether flycatchers chase cowbirds when the flycatchers themselves are far from a nest.

Is aggressive behavior when cowbirds are near the nest maladaptive? Smith et al. (1984) correlated aggressive defense to mounts of female cowbirds with increased incidence of parasitism in Song Sparrows, suggesting that aggressive defense was a maladaptive response. However, in an earlier study, Smith (1981) showed that the reduced fitness in parasitized Song Sparrows is not a result of brood-parasitism per se but a result of egg removal by the cowbird. Thus, the main cost to Song Sparrows occurred when the cowbird intruded and removed the egg. If aggression prevented egg removal, then the enemy recognition and response would be adaptive even if it did not prevent nest discovery. However, this hypothesis that aggressive defense is a counteradaptation to egg removal needs testing.

The relative costs and benefits of host defense differs by host species and the cowbirds' activities. Neudorf and Sealy (1994) comment that prevention of egg predation would be too costly an endeavor for most hosts. Because cowbirds remove eggs throughout the morning hours, hosts would need to defend their nests for long periods of time. If nest guarding precludes foraging, then nest guarding would exact a high cost with little benefit. However, Willow Flycatchers may prove to be an exception. Willow flycatchers can forage near their nests (Uyehara and Narins, pers. observ.) and minimize their foraging time (Ettinger and King 1980, Barlow and McGillivray 1983, Prescott and Middleton 1988). Given their foraging ecology, Willow Flycatchers could stay near their nest throughout the morning, continuously guarding the nest.

Arguably, the most effective counteradaptation to prevent egg predation by cowbirds might be for a bird to sit in the nest (Hobson and Sealy 1989, Burgham and Picman 1989). This is an inconspicuous defense which could deter or delay the egg predatory activities of cowbirds. Our observations and the documented egg removal activities of cowbirds (Scott 1992) suggest that preincubation behavior could act as a defense against the predatory activities of the cowbird intruder, if not the egg-laying activities.

In this population of Willow Flycatchers, not all flycatchers would sit in the nest during cowbird playbacks or during live intrusions or exhibit the behavior inappropriately. The variability in behavior occurred within years which indicates that experimental protocol differences between years did not account for the lack of preincubation behavior. So, although the preincubation behavior is adaptive and exhibited by some individuals, at this time, it is not a specific response to female cowbirds nor do all individuals in this population exhibit this behavior.

Rothstein (1975) hypothesized that hosts which observed cowbirds at their nest might aim nest defense against brood-parasitic intruders. If experience with cowbirds is important (Smith et al. 1984, Briskie et al. 1992, Mark and Stutchbury 1994), then we might expect that parasitized and unparasitized pairs of flycatchers would exhibit differences in their response to cowbirds. Although sample sizes were small, we did not find any evidence that parasitized and unparasitized pairs differed in their response to cowbird intrusions (Table 1; Fig. 3). At this site with high densities of cowbirds (Whitfield, in press), it may be impossible to determine how experience affects Willow Flycatchers. Throughout this study, flycatchers varied in their defensive behavior but we could not determine how previous experience affected the flycatchers' response.

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LITERATURE CITED

Barlow, J. C., and W. B. McGillivray. 1983. Foraging and habitat relationships of the sibling species Willow Flycatcher (*Empidonax traillii*) and Alder Flycatcher (*E. alnorum*) in southern Ontario. Can. J. Zool. 61:1510–1516.

Briskie, J. V., and S. G. Sealy. 1989. Changes in nest defense against a brood parasite over the breeding cycle. Ethology 82:61–67.

Briskie, J. V., S. G. Sealy, and K. A. Hobson. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46(2):334–340.

Burgham, M. C., and J. Picman. 1989. Effect of Brown-headed Cowbirds on the evolution of Yellow Warbler anti-parasite strategies. Anim. Behav. 38:298–308.

Clark, K. L., and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. Wilson Bull. 93:249–258.

Davies, N. B., and M. de L. Brooke. 1988. Cuckoos versus Reed Warblers: adaptations and counteradaptations. Anim. Behav. 36:262–284.

Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. Proc. Royal Soc. Lond. B 205:489–511.

Duckworth, J. W. 1990. Responses of breeding Reed Warblers *Acrocephalus scirpaceus* to mounts of Sparrowhawk *Accipiter nisus,* cuckoo *Cuculus canorus* and jay *Garrulus glandarius.* Ibis 133:68–74.

Ettinger, A. O., and J. R. King. 1980. Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. Auk 97: 533–546.

Folkers, K. L., and P. E. Lowther. 1985. Responses of nesting Red-winged Blackbirds and Yellow Warblers to Brown-headed Cowbirds. J. Field. Ornithol. 56:175–177.

GRAHAM, D. S. 1988. Responses of five host species to cowbird parasitism. Condor 99:588–591.

HARRIS, J. 1991. Parasitism of Willow Flycatchers by Brown-headed Cowbirds in a riparian forest on the Kern River, California. Western Birds 22:13–26.

HARRIS, J., S. D. SANDERS, AND M. A. FLETT. 1987. Willow Flycatcher surveys in the Sierra Nevada. Western Birds 18:27–36.

HOBSON, K. A., AND S. G. SEALY. 1989. Responses of Yellow Warblers to the threat of cowbird parasitism. Anim Behav. 38:510–519.

LAYMON, S. A. 1987. Brown-headed Cowbirds in California: historical perspectives and management opportunities in riparian habitats. Western Birds 18:63–70.

MCCABE, R. A. 1991. The little green bird: ecology of the Willow Flycatcher. Rusty Rock Press, Madison, WI.

MCLEAN, I. G. 1987. Response to a dangerous enemy: should a brood parasite be mobbed? Ethology 75: 235–245.

MCLEAN, I. G., AND G. RHODES. 1991. Enemy recognition and response in birds, p. 173–211. *In* D. M. Power [ed.], Current Ornithology 8:173–211.

MARK, D., AND B. J. STUTCHBURY. 1994. Response of a forest-interior songbird to the threat of cowbird parasitism. Anim. Behav. 47(2):275–280.

MOKSNES, A., AND E. ROSKAFT. 1989. Adaptations of Meadow Pipits to parasitism by the Common Cuckoo. Behav. Ecol. Sociobiol. 24:25–30.

MOKSNES, A., E. ROSKAFT, A. BRAA, L. KORSNES, H. LAMPE, AND H. C. PEDERSEN. 1990. Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour 116(1–2): 64–89.

NEUDORF, D. L., AND S. G. SEALY. 1992. Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? Behaviour 123:84–105.

NEUDORF, D. L., AND S. G. SEALY. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96(1):162–169.

PRESCOTT, D.R.C. 1987. Territorial responses to song playback in allopatric and sympatric populations of Alder (*Empidonax alnorum*) and Willow (*E. traillii*) Flycatchers. Wilson Bull. 99(4):611–619.

PRESCOTT, D.R.C., AND A.L.A. MIDDLETON. 1988. Feeding-time minimization and the territorial behavior of the Willow Flycatcher (*Empidonax traillii*). Auk 105:17–28.

ROBERTSON, R. J., AND R. F. NORMAN. 1976. Behavioral defenses to brood-parasitism by potential hosts of the Brown-headed Cowbird. Condor 78: 166–173.

ROBERTSON, R. J., AND R. F. NORMAN. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). Can. J Zool. 55:508–518.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

ROTHSTEIN, S. I. 1990. A model system for coevolution-avian brood parasitism. Ann Rev. Ecol. Syst. 21:481–508.

ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65(1):77–88.

SANDER, T. G. 1989. Bird songs of California: selected bird songs from the Sierras to the Pacific. Wilderness Recordings, Berkeley, CA.

SCOTT, D. M., P. J. WEATHERHEAD, AND C. D. ANKNEY. 1992. Egg-eating by female Brown-headed Cowbirds. Condor 94(3):579–584.

SEUTIN, G. 1987. Female song in Willow Flycatchers (*Empidonax traillii*). Auk 104:329–330.

SLACK, R. D. 1976. Nest guarding behavior by male Gray Catbirds. Auk 93:292–300.

SMITH, J.N.M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. Condor 83:152–161.

SMITH, J. N. M., P. ARCESE, AND I. G. MCLEAN. 1984. Age, experience, and enemy recognition by wild Song Sparrows. Behav. Ecol. Sociobiol. 14:101–106.

STEIN, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatcher. Proc. Am. Phil. Soc. 107:21–50.

WHITFIELD, M. J. 1990. Willow Flycatcher reproductive response to Brown-headed Cowbird parasitism. M.Sc.thesis, California State Univ., Chico, CA.

WHITFIELD, M. J. In press. Results of a Brown-headed Cowbird control program for the Southwestern Willow Flycatcher. *In* T. Cook, S. Robinson, S. Rothstein, S. Sealy, and J.N.M. Smith [eds.], The ecology and management of cowbirds. Univ. of Texas Press, Austin, TX.

WILEY, J. W. 1988. Host selection by the Shiny Cowbird. Condor 90:289–303.