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EFFECTS OF NEST PARASITISM BY THE BROWN-HEADED COWBIRD ON NESTING SUCCESS OF THE CALIFORNIA GNATCATCHER[1]

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Abstract. California Gnatcatcher (*Polioptila californica californica*) nests, from 1992–1995 at five sites in western Riverside County, California, were examined to determine the effects of Brown-headed Cowbird (*Molothrus ater obscurus*) nest parasitism and cowbird trapping on nest fates. Before cowbird trapping, nest parasitism was 31.5% over the entire breeding season and 45.7% during the period when cowbirds were active. Nest parasitism appeared to decrease gnatcatcher nest success by increasing nest abandonment. However, nests were lost to depredation versus parasitism at a 3:1 ratio. Gnatcatcher eggs were significantly correlated with cowbird eggs beginning the week of 5 May in 1992 and 1993, indicating the onset of parasitism pressure within a breeding season. Considering nests initiated after 5 May, nest parasitism was significantly reduced from 45.7% before cowbird trapping to 9.8% after cowbird trapping, and nest success increased significantly from 11.2% before cowbird trapping to 21.7% after cowbird trapping. Considering nest fates regardless of initiation date, there were no significant differences between no-trap and trap periods. Comparisons of no-trap versus trap nest fates before 5 May indicated that nest abandonment increased significantly from 3.3% for the no-trap period to 28.7% during the trapping period. At the same time, nest success decreased significantly from 35.0% during the no-trap period to 15.7% during the trap period. Gains in nest success from decreased nest parasitism were negated by increased nest abandonment before cowbirds were active.

Key words: Polioptila californica, *California Gnatcatcher,* Molothrus ater, *Brown-headed Cowbird, parasitism, nest success.*

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater obscurus*) is an obligate nest parasite that parasitizes the nests of resident and migratory passerines (Friedmann and Kiff 1985). Some hosts fledge their own nestlings along with cowbird nestlings (Ortega and Cruz 1992, Smith and Arcese 1994), whereas other hosts rarely are successful in fledging their own young if cowbird nestlings are present (Graber 1961, Marvil and Cruz 1989). The ability of the host to fledge its own, as well as cowbird young, may depend on differences in host versus parasite nestling age (Marvil and Cruz 1989) or body size (Ortega and Cruz 1992). High parasitism rates have been associated with habitat fragmentation (Robinson 1992, Brawn and Robinson 1996), and nest parasitism has been inferred to be a major factor in the decline of many passerines, including endangered or threatened species (Mayfield 1977, Nolan 1978). Cowbird trapping may reduce nest parasitism but does not necessarily result in an increase in host populations (Kelly and DeCapita 1982, Smith and Arcese 1994).

The California Gnatcatcher (*Polioptila californica californica*) is a small sedentary Certhiid warbler (Sibley and Monroe 1990) endemic to the coastal sage scrub community of southern California and northern Baja California, Mexico (Atwood 1991). The California Gnatcatcher is federally listed as a threatened species. Current population estimates are in the vicinity of 2,000 pairs for the United States; the decline of the gnatcatcher has been concomitant with the disappearance and degradation of coastal sage scrub habitats (Atwood 1992, 1993). The coastal sage scrub community is a Mediterranean type habitat typified by facultatively drought deciduous mesophilic shrubs from 0.5 m to 2.0 m tall (Westman 1981, Mooney 1988). The coastal sage scrub community has been heavily affected

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by agriculture, exotic weeds, increased fire frequency, air pollution, livestock grazing, and urban expansion (Klopatek et al. 1979, Westman 1985, O'Leary 1990).

Nest parasitism of the California Gnatcatcher by the Brown-headed Cowbird began as early as 1933, based on egg sets from the San Bernardino County Museum, San Bernardino, California, and is consistent with the documented increase in Brown-headed Cowbird populations detailed by Mayfield (1977). Here we examine the effects of nest parasitism on California Gnatcatcher nesting success by comparing gnatcatcher nest fates for parasitized and unparasitized nests and nest fates before and after cowbird trapping.

METHODS

DATA COLLECTION

Gnatcatcher nests were monitored at Lake Skinner from 1992 through 1995, Lake Mathews from 1993 through 1995, the University of California Motte Rimrock Ecological Reserve from 1993 through 1994, and two additional sites, North Hills and South Hills of the Domenigoni Valley near Lake Skinner, during 1992. All five study sites were located in western Riverside County, California (Fig. 1).

Adult gnatcatchers were uniquely color banded at the beginning of the study and as needed at the onset of each breeding season. Gnatcatcher nestlings were banded on the nest when they were 8 days old. All observations involved banded birds. Territories were visited two to four times a week throughout the breeding season which extended from late February or early March, to early July or early August, depending on the year and the site. Nests were visited at 2 to 4 day intervals and monitored for the onset of egg laying, clutch size, nest parasitism, number of nestlings, and number of fledglings. The frequency of nest visits was the same at each site and throughout the study. Three cowbird traps were located at Lake Mathews, five traps at Lake Skinner, and two traps at the Motte. Cowbird traps were modified Australian Crow traps, baited with wild bird seed and two to four live cowbirds. Traps were visited every day in 1994 from early March through late July. In 1995, the trapping period was the same but trap checks were less frequent and often involved nonbiologists, resulting in a few cowbirds being

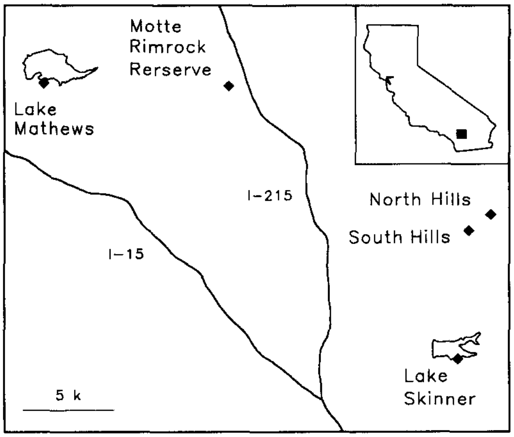

FIGURE 1. Five study areas in western Riverside County monitored for California Gnatcatcher nest fates from 1992 through the 1995 breeding seasons. Scale is approximate.

released or miscounted. Cowbird trapping began in 1994 and continued through 1995 resulting in two breeding seasons with no cowbird trapping (1992 and 1993) and two breeding seasons with cowbird trapping (1994 and 1995).

Nest fates were categorized as parasitized, depredated, abandoned, or successful. The latter three categories were mutually exclusive but none were exclusive of parasitism. A nest was considered successful if one or more nestlings fledged. Since nestlings were banded on the nest when they were 8 days old, the exact or at least approximate fledging dates were known. Nests were considered depredated if some or all of the eggs had disappeared, eggs had been damaged, or there were eggs or eggshell fragments in the vicinity of the nest, and as long as the adult birds no longer tended the nest. Shredded or damaged nest structures were always interpreted as nest depredation. Nests were considered abandoned when nests indicated no sign of predation but were no longer tended by the parents. Nests were classified as parasitized based on the presence of a cowbird egg in the nest or an appropriately sized puncture of a gnatcatcher egg. Egg punctures were compared to cowbird bill size to differentiate between punctures due to cowbirds versus other passerines such as wrens. Classification of a nest as parasitized based solely on an egg puncture was a rare event. This classification method probably underestimated the effects of cowbirds on gnatcatcher nests because cowbirds are known to remove a host's egg without depositing their own (Scott et al. 1992).

PARASITISM AND NEST FATES

The effects of parasitism on gnatcatcher nests were examined through a comparison of depredated, abandoned, and success gnatcatcher nests for parasitized and unparasitized nests during the no-trap period. Comparisons were made by contingency tables with Yates' correction following Zar (1984).

COWBIRD TRAPPING AND NEST FATES

California Gnatcatchers are resident passerines that begin nesting long before cowbirds begin laying eggs in hosts' nests. Because the purpose of this study was to compared the influence of nest parasitism on gnatcatcher nest fates, it was necessary to determine the point during the breeding season when nest parasitism could conceivably influence gnatcatcher nest fates. Nest parasitism increased in frequency from the middle of April to the middle of May, after which parasitism was fairly constant compared to the number of gnatcatcher nests. The weekly totals of gnatcatcher eggs and cowbird eggs were correlated beginning the week of 5 May each year, which effectively divided the breeding season into early and late periods. The early period (before 5 May) corresponded to an overall lack of nest parasitism. The late period (after 5 May) corresponded to the period of significant nest parasitism. The mean date of the first nest parasitism during 1992 and 1993 was the week previous to 5 May, but the correlation between the number of cowbird and gnatcatcher eggs was not significant. Thus, the week of 5 May was chosen as the initiation of the nest parasitism phase of the breeding period. Six nests parasitized prior the week of 5 May and six nests with incubation periods overlapping the week of 5 May were eliminated from all analyses. The slopes and intercepts of the 1992 and 1993 correlations of gnatcatcher and cowbird eggs were tested for differences before combining samples.

Weekly totals of eggs, instead of nests, were chosen as the sample unit for correlations of cowbird and gnatcatcher eggs for several reasons. The determination of the weekly number of nests subject to parasitism was not accurate. Some nests were found when they were first initiated, and therefore the weeks during which these nests could have been parasitized were known. Other nests were not found until a complete clutch was laid, but were depredated before the eggs hatched, so it was not possible to determine the number of weeks the nest was present. Cowbirds do not build nests, so nests could not be used as the sample unit for both cowbirds and gnatcatchers.

Gnatcatcher nest fates were compared using multiway contingency tables (BMDP 1992) to determine at which level (model), if any, nest fates were influenced by trapping or parasitism treatments. Nest fates were configured into the table as: (depredated or not depredated, abandoned or not abandoned, successful or not successful) × (no-trapping versus trapping) × (before 5 May, cowbirds not active, versus after 5 May, cowbirds active). Based on the results from the multiway contingency table, nest fates were grouped into two-by-two contingency tables with Yates' correction as appropriate following Zar (1984). For the no-trapping period, two-by-two comparisons were made between nests classified as depredated or not depredated, abandoned or not abandoned, and successful or not successful for before and after 5 May in order to identify potential effects of nest parasitism on gnatcatcher nest fates. For the trapping period, the same two-by-two comparisons were made to determine if the effects of nest parasitism had been eliminated by cowbird trapping. Overall nest fates, defined as the fates of all nests regardless of initiation date, were compared to determine if a significant reduction in nest parasitism had an overall effect on gnatcatcher nest fates, especially nest success. Nests fates for no-trap and trap periods were compared after 5 May in order to determine if a significant reduction in nest parasitism had an effect on gnatcatcher nest fates for the period when nest parasitism was significant. Nest fates were compared before 5 May for the no-trap and trap periods in order to determine if factors other than nest parasitism could be influencing gnatcatcher nest fates. Finally, gnatcatchers may abandon nests as a means of dealing with nest parasitism, so contingency tables were used to determine if gnatcatchers abandoned parasitized nests more often than unparasitized nests.

Heterogeneity tests were used before combining sites between years for the no-trap and trap periods. Because study sites varied outside of the 1993 and 1994 breeding seasons, analyses were performed using 1993 and 1994 data, and contrasted with results using 1992 and 1995 data.

RESULTS

PARASITISM AND NEST FATES

Of the 168 nests observed from 1992 through 1993, 54.2% were depredated, 31.5% were parasitized, 22.6% were abandoned, 17.9% were successful, and 5.4% were lost due to weather or infertility (Table 1). There was no significant difference in depredation of parasitized nests (45.3%) and unparasitized nests (58.3%) (χ^2_1 = 1.97). Abandonment was significantly higher in parasitized (41.5%) than unparasitized nests (13.9%) ($\chi^2_1 = 14.2$, $P < 0.001$). Abandonment of unparasitized nests was significantly lower than depredated unparasitized nests ($\chi^2_1 = 47.1$, $P < 0.001$). The percentage of abandoned parasitized nests did not differ from depredated parasitized nests ($\chi^2_1 = 0.04$). Nest success was significantly lower for parasitized nests (0%) than for unparasitized nests (26.1%; $\chi^2_1 = 15.1$, $P < 0.001$). Thus, nest parasitism appears to decrease nest success by increasing nest abandonment. Nevertheless, more nests were lost to predation (54.2%) than to parasitism (17.3%; $\chi^2_1 = 48.2$, $P < 0.001$). Nests were lost to predation versus parasitism at a 3:1 ratio.

Gnatcatchers were never observed to eject or damage cowbird eggs. Cowbird eggs were never observed in the vicinity of a nest except in cases where nest predation was apparent. Cowbird eggs never disappeared from a parasitized nest except in three instances where marked cowbird eggs had been replaced by unmarked cowbird eggs, presumably by a cowbird. Gnatcatchers never fledged from unmanipulated parasitized nests, and in only one event did gnatcatcher eggs hatch in the presence of a cowbird egg. Examination of gnatcatcher embryos from an abandoned parasitized nest showed asynchronous development with a 3-day disparity in maximum and minimum development. Cowbird eggs are approximately twice the size of gnatcatcher eggs, which may cause problems in gnatcatchers maintaining body contact with their own eggs during incubation of parasitized nests.

COWBIRD TRAPPING AND NEST FATES

There were no significant differences in slopes or intercepts for correlations of cowbird versus gnatcatcher eggs beginning the week of 5 May in 1992 versus 1993 ($F_{2,18} = 2.3$, $n = 21$), so data sets were combined. For the combined years, the number of gnatcatcher eggs laid per week were significant predictors of the number of cowbird eggs found in gnatcatcher nests per week beginning the week of 5 May through the end of the breeding seasons ($r^2 = 0.52$, $P < 0.001$, $n = 21$).

There were no significant differences in heterogeneity tests among sites or between years for the no-trap (1992–1993) period, so data were combined. Likewise, there were no differences within the trapping period (1994–1995), so data were combined. There were no significant differences in overall results using 1993 and 1994 data alone, where study sites were the same, versus data from 1992 and 1995 alone, where some of the study sites were different.

Multiway contingency analysis indicated that contingencies ($P < 0.005$) were likely to exist in second order models that compared nest fates among no-trap versus trap years, and nest fates before 5 May versus after 5 May. All third order models were not significant ($P > 0.05$). All 12 two-way comparisons involving nest fates grouped by trapping and periods of nest parasitism were examined. Despite the number of comparisons, the alpha value to denote significance was left at $P \leq 0.05$, because the multiway contingency table indicated that several two-factor interactions were likely to be significant.

During the no-trap period, nest predation was not different before versus after the annual onset of nest parasitism (5 May). For the same period, nest abandonment increased significantly from 3.3% before the onset of nest parasitism to 31.8% after the annual onset of nest parasitism.

TABLE 1. Fates of parasitized and unparasitized nests of the California Gnatcatcher during the 1992 and 1993 breeding seasons at five sites in western Riverside County, California.

	Not parasitized	Parasitized	Total
Nests	115	53	168
Depredated	67	24	91
Abandoned	16	22	38
Successful	30	0	30
Unknown[a]	2	7	9
Gnatcatcher eggs	270	109	379
Gnatcatchers fledged	112	0	112
Cowbird eggs	—	73	73
Cowbirds fledged	—	2	2

[a] Nests failed due to weather, infertility, or undetermined causes.

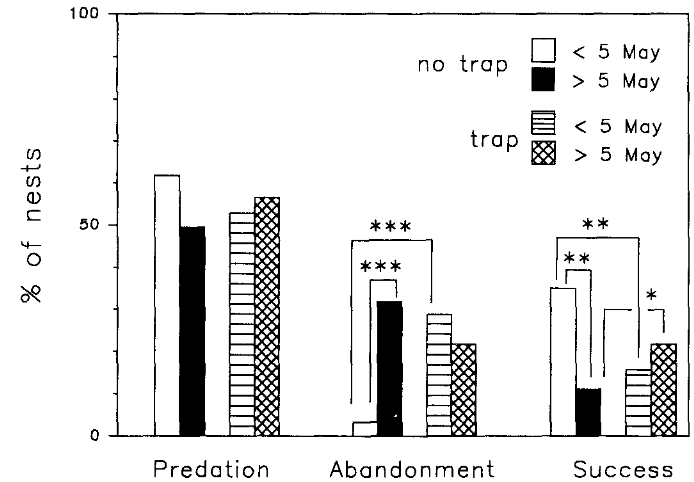

FIGURE 2. Comparisons of depredated, abandoned or successful gnatcatcher nests, before and after cowbird trapping, and before and after the annual onset of nest parasitism (5 May). See text for justification of 5 May as the annual onset of nest parasitism. Sample sizes for no-trap < 5 May = 60, no trap > 5 May = 107, trap < 5 May = 108, and trap > 5 May = 138. (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$)

At the same time, nest success decreased significantly from 35.0% before the onset of nest parasitism to 11.2% after the annual onset of nest parasitism (Fig. 2). Nest parasitism was significantly reduced from 45.7% (49/107) during the no-trap period after 5 May to 9.8% (13/132 nests) during the trap period after 5 May (χ^2_1 = 37.9, $P < 0.001$, n = 239).

During the trap period, there was no significant difference in nest predation before versus after the annual onset of nest parasitism. Nest abandonment and nest success did not differ before versus after the annual onset of nest parasitism (Fig. 2).

Contrary to expectations based on the significant reduction of nest parasitism and the within period (before and after 5 May) comparisons of nest fates for no-trap and trap periods, there was no overall significant increase in the number of successful gnatcatcher nests. Comparisons of gnatcatcher nest fates for no-trap versus trap periods indicated a profound lack of change in nest depredation (χ^2_1 = 0.01, n = 413), nest abandonment (χ^2_1 = 0.41) and nest success (χ^2_1 = 0.001).

Comparisons of nest fates for no-trap and trap periods, after the annual onset of nest parasitism, indicated no significant differences before versus after trapping for nest predation or abandonment. However, there was a small but significant increase in nest success from 11.2% before cowbird trapping to 21.7% after cowbird trapping (Fig. 2).

Comparisons of no-trap and trap nest fates, prior to the annual onset of nest parasitism, indicated no significant differences in nest predation. However, nest abandonment increased significantly from 3.3% during the no-trap period to 28.7% during the trap period. At the same time, nest success decreased significantly from 35.0% during the no-trap period to 15.7% during the trap period (Fig. 2).

For the no-trapping period, after the onset of nest parasitism, nest abandonment was significantly higher for parasitized nests (36.7%, 18/49) than for unparasitized nests (18%, 9/50; Fisher Exact Test, P = 0.03, n = 99). Gnatcatchers abandoned 36.7% of parasitized nests, whereas 63.3% (31/49) of parasitized nests were not abandoned.

COWBIRD TRAP SUCCESS

In 1994, cowbird trapping resulted in 100 male, 40 female, and 27 juvenile cowbird captures. In 1995, cowbird trapping resulted in 137 male, 129 female, and 74 juvenile cowbirds reported as captured. The error in the total number, age and sex of cowbird captures in 1995 is probably less than 20%, based on the frequency of trap visits by experienced versus inexperienced personnel. An error rate of 50% in the number of cowbird captures in 1995 would result in a minimum of 68 male and 64 female captures, which is still 24 more adult female cowbirds captured in 1995 than in 1994.

DISCUSSION

Both predation and nest parasitism affected gnatcatcher nest fates, but predation had a greater influence than parasitism. Overall, gnatcatcher nest losses due to predation were three times those due to nest parasitism. Approximately half of the potential impact of nest parasitism on gnatcatcher nest fates were negated by depredation of parasitized nests.

A secondary role of nest parasitism is more firmly supported through comparisons of gnatcatcher nest fates relative to cowbird trapping. Nest success decreased from 35.0% before 5 May to 11.2% after 5 May in the absence of cowbird trapping. At the same time, nest abandonment increased from 3.3% before 5 May to 31.8% after 5 May. Differences in nest abandonment and success before and after 5 May were no longer apparent after trapping, and nest parasitism had been significantly reduced. After the onset of nest parasitism, gnatcatcher nest success increased significantly from 11.2% during the no-trap period to 21.7% during the trap period, suggesting that nest parasitism has a negative effect on gnatcatcher nest success. However, overall gnatcatcher nest fates, including nest success, did not change even though nest parasitism had been significantly reduced and despite a small but significant increase in nest success.

The cause of this apparent contradiction had to do with significant differences in nest abandonment and nest success before and after trapping that occurred before cowbirds were active. Nest abandonment, before the annual onset of nest parasitism, increased significantly from 3.3% before trapping to 28.7% after trapping. At the same time, nest success decreased significantly from 35% before trapping to 15.7% after trapping. Thus, modest gains in nest success which could reasonably be attributed to a decrease in nest parasitism were overwhelmed by a large decrease in nest success, probably due to nest abandonment, which had nothing to do with nest parasitism because it occurred before cowbirds were active. Therefore, factors other than nest parasitism were having a greater influence on nest success. Nest success during the trapping period, after 5 May, could have shown a significant decline, rather than a modest increase, were it not for the reduction in nest parasitism. However, increases in the number of successful nests, due to a reduction of nest parasitism, would have to be substantial to compensate for the number of nests lost to abandonment or predation before cowbirds were active.

Rohwer and Spaw's (1988) and Rothstein's (1990) proposed mechanism by which antiparasite strategies, that include nest abandonment, should be selected for, if parasitism has a strong negative influence on a host's reproductive success. However, support for the hypothesis that gnatcatchers use nest abandonment as an adaptive strategy to deal with nest parasitism was weak. First, gnatcatchers abandoned parasitized nests significantly more often than unparasitized nests, but 63.3% of parasitized nest were not abandoned. Some of those abandoned nests were likely abandoned for reasons other than parasitism. If abandonment of parasitized nests is an adaptive mechanism, it is not very effective, at least not yet. Nest abandonment as an adaptive response to nest parasitism cannot be assumed until nest abandonment in response to a foreign object can be discounted. Second, this study suggests that the selective pressure for gnatcatchers to evolve antiparasite strategies may be low. Approximately half of the parasitized nests were eliminated by nest predation, so half of the negative consequences of nest parasitism were not expressed and could not be selected against. Increased nest success due to reduced nest parasitism was small compared to decreased nest success due to abandonment and predation. Therefore selection pressures should be greater for mechanisms to reduce nest abandonment and predation than for mechanisms to reduce nest parasitism. Antiparasite mechanisms would be potentially useful and selected for during only half of the breeding season because gnatcatchers begin nesting two months before cowbirds are active. Therefore, even if low selection pressure for antiparasite behaviors resulted in behavioral changes, such behaviors would probably spread slowly through the population because half of the breeding season occurs when there is no selection for the behavior. These observations and the results of this study suggest that nest parasitism for resident open-cup nesters that begin breeding before cowbirds are active may not be important relative to other causes of nest failure.

Therefore, antiparasite defense mechanisms are likely to evolve slowly if at all.

Although gnatcatcher nest predation and abandonment were more important than nest parasitism to nest success, the causes of nest predation and abandonment cannot be determined from this study. Direct observation and the condition of depredated nests suggest that gnatcatcher nest predators are diverse. Known or suspected gnatcatcher nest predators include gopher snake (*Pituophis melanoleucus*), king snake (*Lampropeltis getulus*), coachwhip (*Masticophis flagellum*), Beechey ground squirrel (*Spermophilus beecheyi*), deer mouse (*Peromyscus maniculatus*), coyote (*Canis latrans*), long-tailed weasel (*Mustela frenata*), Roadrunner (*Geococcyx californianus*), and Bewick Wren (*Thryomanes bewickii*). Annual variation in predator diversity, abundance, and activity is likely to result in annual variation in gnatcatcher nest depredation. Assuming that the presence of a predator in close proximity to a nest will result in nest abandonment, variation in predator composition also could account for annual variation in nest abandonment. Annual variation in weather conditions also is likely to influence nest abandonment and predation, especially early in the breeding season. The climate of southern California is typified by cool wet winters followed by hot dry summers, and rainstorm frequency decreases as the breeding season progresses. Variability in the frequency or duration of late season storms could affect abundance, activity, and diversity of heterothermic predators, which in turn should influence nest abandonment and predation early in the breeding season.

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