

EFFECTS OF FEMALE COWBIRD REMOVAL ON REPRODUCTIVE SUCCESS OF HOODED WARBLERS

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ABSTRACT.—Female Brown-headed Cowbirds (*Molothrus ater*) were systematically removed from two adjacent Hooded Warbler (*Wilsonia citrina*) breeding populations for 2–5 years. All female cowbirds detected using playbacks were removed. Although an average of only 17 female cowbirds were removed annually from each population, this reduced the frequency of parasitism to < 10% of nests in most years. The average percentage of nests parasitized (53%) in populations with no cowbird control (N = 3) was significantly higher than for populations where female cowbirds were being removed (9%, N = 7). Experimental reduction of parasitism, however, did not result in a significant increase in number of young fledged per nest. Predation of entire clutches and broods effectively swamped the gains achieved by controlling female cowbirds. The effectiveness of cowbird removals as a management tool will likely vary with cowbird abundance and host species, but this study suggests that beneficial effects for the host species can be minimal. Received 27 Feb. 1996, accepted 20 Aug. 1996.

The alarming decline of many North American songbird populations over the past few decades (Robbins et al. 1989, Askins et al. 1990) has led to intensified efforts to identify the causes of this decline (e.g., Hagan and Johnston 1992). There is much debate about whether the critical factor causing the songbird decline is loss of winter habitat (e.g., Robbins et al. 1989) or fragmentation of breeding habitat (e.g., Robinson et al. 1995b, Sherry and Holmes 1996). Brown-headed Cowbirds (*Molothrus ater*) have been implicated in the songbird decline (e.g., Brittingham and Temple 1983, Robinson et al. 1995b) because they are brood parasites of songbirds. Forest fragmentation in eastern North America, combined with an increase in cowbird numbers (Brittingham and Temple 1983), has led to unusually high rates of brood parasitism on many forest songbirds (e.g., Robinson et al. 1995b).

There have been calls to control cowbird populations on a large scale as a management tool for slowing population declines (Robinson et al. 1995b). However, few studies have actually controlled adult cowbirds and assessed the impact on songbird breeding success. In the most famous example, cowbird control in the Kirtland's Warbler (*Dendroica kirtlandii*) breeding area decreased parasitism and increased the average number of young fledged per nest (Kelly and DeCapita 1982, Walkinshaw 1983), but this did not lead to an increase in population numbers (Mayfield 1993). Cowbird control programs for the Least Bell's Vireo (*Vireo belii pusillus*) and Black-capped Vireo (*V. atricapillus*) have also reduced par-

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asitism and increased nesting success (reviewed in Robinson et al. 1995a). Cowbird removals are apparently linked to increasing populations of the Least Bell's Vireo and Willow Flycatcher (*Empidonax traillii extimus*) (reviewed in Robinson et al. 1995a). In this study, I examined the effectiveness of female cowbird removals for increasing the reproductive success of Hooded Warblers (*Wilsonia citrina*), a species that is not threatened and has extensive breeding habitat remaining. The frequency of brood parasitism and nesting success of Hooded Warblers in a cowbird removal area was compared with populations without cowbird control.

METHODS

I conducted this study from 1991–1995 in Crawford County, Pennsylvania (41°N, 79°W), in conjunction with other on-going research (Stutchbury et al. 1994, Neudorf 1996, Tarof 1996, Stutchbury and Evans Ogden 1996). The main study site of 100 ha mixed hardwood forest supports about 40 breeding pairs annually. Another study area (50 ha) continuous with the main study site was included, beginning in 1994, and supported an additional 20 pairs. In 1994 and 1995 we also located breeding Hooded Warblers in several nearby forests (10–30 ha) where no cowbird control was done. Nesting adults were banded with U.S. Fish and Wildlife Service bands and color banded. We found nests at the building, egg-laying, or incubation stage, usually by following the female to the nest. We checked nests every 3–5 days to determine nesting success. All cowbird eggs were removed from nests. Nestlings were banded, and in many cases, blood samples were taken for use in DNA fingerprinting (Stutchbury et al. 1994). Cowbird parasitism frequency in the main study area for the years 1984–90, prior to the cowbird removals, were obtained from studies by E.S. Morton (unpubl. data).

Female cowbirds were removed by shooting from late April through mid-June. From 07:00–11:00 h EST, playbacks of the female “chatter” call were used to lure female cowbirds to the speaker (e.g., Dufty 1982, Yokel 1989). This also attracted male cowbirds. Beginning the first week of May, and about once per week, 3-min playbacks were performed every 100 m along a circuit through the study site. Cowbirds were collected with a shotgun. In most years, a comparable number of male cowbirds (15–20) were also removed because unmated males could potentially attract females to the area. Relatively few males (< 10) were removed in 1995 because the removal of females alone appeared sufficient for reducing parasitism rates.

RESULTS

An average of 17 female cowbirds were removed from each population per year (Table 1). Cowbirds were most abundant in May, and few females were seen or heard after mid-June. Most (56%) female cowbirds were removed during the first two weeks of May, and only a few (16%) were removed in June. Cowbirds were removed throughout the study site, including the locations most distant (500 m) from the forest edge.

Although only 8–30 female cowbirds were removed annually from each population, this likely represented most of the breeding females. Removals on this scale were highly effective in reducing parasitism on Hooded Warbler nests. The frequency of cowbird parasitism in the main

TABLE 1
NUMBER OF MALE AND FEMALE COWBIRDS REMOVED EACH YEAR AND PERCENTAGE OF NESTS PARASITIZED IN EACH HOODED WARBLER POPULATION

Population (# nests)	Cowbirds removed		Parasitism frequency
	Male	Female	
Brown Hill			
1984–1990 (28)	0	0	64%
1991 (45)	9	13	0%
1992 (62)	26	15	13%
1993 (56)	15	29	34%
1994 (40)	29	31	3%
1995 (38)	4	12	5%
Morton Farm			
1994 (22)	12	8	0%
1995 (17)	3	14	6%
Berlin			
1994 (8)	0	0	38%
1995 (24)	0	0	58%

Brown Hill population was 64% (18 of 28 nests) prior to the removals (Table 1). The parasitism frequency was low (0–13%) in the Brown Hill population most years of the removals, except 1993. Parasitism was also very low (< 10%) in the adjacent Morton Farm population in both years of removals (Table 1). The average level of parasitism in populations where female cowbirds were removed (9%, $N = 7$) was significantly lower (Mann-Whitney U -test, $z = 2.39$, $P < 0.05$) than for the populations with no cowbird control (53%, $N = 3$).

Both clutch size and number of young hatched were significantly higher for nests in areas where parasitism was reduced to $\leq 5\%$ of nests (Table 2). The average number of young fledged from all nests (including those preyed upon) in areas with very low parasitism was not significantly ($t = 0.53$, $P > 0.50$) higher than for populations with high parasitism (Table 2). The number of young fledged per nest did not vary significantly with the percentage of nests parasitized (Fig. 1; $r^2 = 0.16$, $P^2 = 0.28$). Predation frequency varied from 22%–52% among populations, so many nests that escaped parasitism were preyed upon. The frequency of predation did not vary consistently with parasitism frequency ($r^2 = 0.16$, $P = 0.29$).

Predation on entire broods effectively removed the increase in nesting success that would be expected if cowbird parasitism were absent. This

TABLE 2
CLUTCH SIZE, NUMBER HATCHED AND NUMBER FLEDGED FOR HOODED WARBLER NESTS IN POPULATIONS WITH VERY LOW PARASITISM ($\leq 5\%$ NESTS) AND HIGH PARASITISM ($>30\%$)^a

Variable	All nests		Successful nests	
	Low (N = 145)	High (N = 88)	Low (N = 81)	High (N = 51)
Clutch size	3.60 (0.62)**	3.08 (0.92)	—	—
No. hatched	2.43 (1.62)*	1.74 (2.63)	3.32 (0.88)**	2.57 (1.30)
No. fledged	1.72 (1.75)	1.60 (1.55)	3.20 (0.96)*	2.74 (0.98)

^a Means (SD) are given for all nests (including those preyed upon), and for successful nests (those that escaped predation). Statistical significance for *t*-tests indicated by asterisks (** $P < 0.001$, * $P < 0.05$).

can be seen by comparing the productivity of only those pairs whose nest was not preyed upon. Hooded Warbler pairs breeding in areas with low parasitism had an average of 3.20 ± 0.96 young per nest, significantly higher than the 2.74 ± 0.98 young for areas with high parasitism (Table 2). As expected, number of young fledged from successful nests was significantly correlated with percentage of nests parasitized (Fig. 1; $r^2 = 0.60$, $P = 0.01$).

To determine if cowbird removal increased average reproductive success compared with Hooded Warbler populations in other parts of the breeding range, nesting data were obtained from other researchers (Arkansas, T. Martin; Ohio, R. Dettmers; Ontario, M. Gartshore). The number of young fledged from these three populations was compared to the Pennsylvania populations where cowbird parasitism was experimentally reduced to \leq

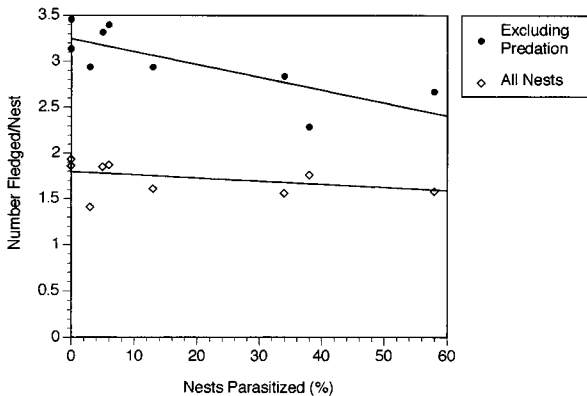


FIG. 1. Mean number of young fledged per nest (for all nests and for only those that escaped predation) for each Hooded Warbler population versus the percentage of nests parasitized.

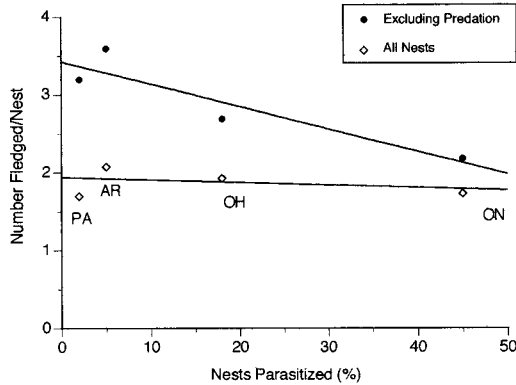


FIG. 2. Mean number of young fledged per nest (for all nests and only those that escaped predation) for the Pennsylvania populations with $\leq 5\%$ parasitism ($N = 145$ nests) and for populations in Arkansas ($N = 99$), Ohio ($N = 82$) and Ontario ($N = 28$).

5% (Fig. 2). Number of young fledged per nest did not vary with the percentage of nests parasitized. In these studies, predation frequency was highest (48%) for Pennsylvania, modest for Arkansas (39%) and Ohio (30%) and relatively low for Ontario (21%). Reproductive success in the Pennsylvania population where cowbirds were controlled was similar to that of the Arkansas population where parasitism rates are naturally low (Fig. 2). When predation was removed as a factor, the expected correlation between reproductive success and parasitism was clear (Fig. 2).

DISCUSSION

There are two main findings of this cowbird removal experiment. First, removing a small number of female cowbirds each year early in the breeding season dramatically reduced parasitism rates on Hooded Warblers. Second, removal of female cowbirds did not result in a significant increase in reproductive success.

Most cowbird removal experiments have been successful in reducing the frequency of cowbird parasitism (reviewed in Robinson et al. 1995a). The scale of the cowbird removals clearly depends on the size of the breeding area and the density of cowbirds. The Kirtland's Warbler project removed over 1000 female cowbirds per year using drop-in traps located throughout the 4000-ha breeding areas (Walkinshaw 1983). In the present study, playbacks of female cowbird calls were used to attract local females that were likely to parasitize nests within the 150 ha removal site. Although only a modest number of females were removed per population, this apparently represented almost the entire breeding population of cow-

birds. Female cowbirds removed early in the season were replaced by other individuals, so it is difficult to estimate the local density of cowbirds. The maximum estimate of female cowbird density is about 20/km² for the Brown Hill and Morton Farm populations, which is at the low end of range reported for cowbirds (Yokel 1989). Whether such small scale cowbird removal would be equally successful in reducing parasitism in regions of high cowbird density is not known. There was no evidence that removals in one year had any carry over effect in terms of reducing cowbird numbers the subsequent year.

Although cowbird removals dramatically increased reproductive success by 0.8–1.9 fledglings per nest in the Kirtland's Warbler (Kelly and DeCapita 1982), Least Bell's Vireo, and Black-capped Vireo (reviewed in Robinson et al. 1995a) this was not the case for Hooded Warblers. Clutch size and number of young hatched were significantly higher for nests in populations with very low parasitism (Table 2), reflecting the low frequency of egg losses due to cowbirds. Number of young fledged, however, was not significantly higher for populations with low parasitism due to the effects of nest predation (Fig. 1, Table 2). Cowbird removal resulted in an average increase of only 0.12 young fledged per Hooded Warbler nest. To put this into perspective, this amounts to about five extra fledglings produced from a population of 40 breeding pairs of Hooded Warblers.

When compared with several Hooded Warbler populations across the breeding range (Fig. 2), cowbird parasitism was not significantly related to number of young fledged per nest. Variability in predation frequency among populations tended to overshadow small differences in reproductive success that resulted from cowbird parasitism. These results suggest that cowbird removals on a large scale to reduce parasitism may not result in any significant increase in productivity of Hooded Warblers. Cowbird removal may have minimal advantages in other species too, because predation often causes much higher daily mortality on nests than does parasitism (Donovan et al. 1995).

Cowbird removals may be more likely to benefit host species in areas with extreme forest fragmentation and many cowbird eggs per host nest (e.g., Robinson et al. 1995a). Also, some species fledge few of their own young when parasitized (e.g., Walkinshaw 1983), so cowbird parasitism can outweigh predation as a leading cause of nest mortality. Clearly, removal of cowbirds in specific populations of endangered and threatened species can increase reproductive success of particular host species (Walkinshaw 1983, Robinson et al. 1995a). Small scale removals of cowbirds in specific research areas can also be valuable for studying the behavior and ecology of songbirds in the absence of parasitism. Studies of the

evolution of parental care, fledgling care, and extra-pair mating tactics in eastern forest songbirds (e.g., Stutchbury et al. 1994, Neudorf 1996, Stutchbury and Evans Ogden 1996, Tarof 1996) are hampered by unnaturally high levels (40–60%) of brood parasitism. The effectiveness of cowbird removals as a management tool will likely vary with cowbird abundance and host species, but this study indicates that beneficial effects for the host species can be minimal.

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