

## HOW DO BROWN-HEADED COWBIRDS (*MOLOTHRUS ATER*) CAUSE NEST FAILURES IN SONG SPARROWS (*MELOSPIZA MELODIA*)? A REMOVAL EXPERIMENT

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**ABSTRACT.**—A removal experiment was conducted to measure how much and by what mechanisms brood parasitic Brown-headed Cowbirds (*Molothrus ater*) cause nest failures in a commonly used host, the Song Sparrow (*Melospiza melodia*). When numbers of female cowbirds were reduced experimentally, nest failures fell from 65.0% ( $n = 663$  nests) to 49.9% ( $n = 331$ ). Cowbird reduction reduced the frequency of nest failure to one-third of control levels in Song Sparrows during the last 80 days of the sparrow's breeding season, the period when most parasitic laying took place. Cowbird reduction decreased nest failures strongly at the egg stage, and weakly at the nestling stage. Daily nest-failure rates were independent of whether or not a nest was parasitized by cowbirds. Two hypotheses were tested to explain how cowbirds cause host nests to fail: first, egg removal by female cowbirds lowers clutch size below a threshold where the host deserts; second, cowbirds cause host nests to fail by destroying entire clutches or broods. In support of the first hypothesis, desertion following parasitism and egg removal was less frequent when cowbird numbers were reduced (8.9% of  $n = 158$  nests) than for unmanipulated controls (16.5% of  $n = 424$  nests). In support of the second hypothesis, there were fewer cases where young were killed in the nest, or found dead near it, after cowbird numbers were reduced (2.5% of 158 nests) than in controls (4.7% of 424 control nests). In contrast, proportions of nests that failed after the disappearance of all eggs, young, or both, and after unparasitized clutches were deserted, increased when cowbird numbers were reduced. Although our study supports both hypotheses, cowbird-induced desertion had a greater effect on nest failure rates than did cowbird predation. Our study suggests that cowbird removal programs are likely to benefit commonly used and endangered hosts by reducing rates of nest failure. Received 21 August 2002, accepted 5 February 2003.

**RESUMEN.**—Realizamos un experimento de remoción para medir cuánto y por qué mecanismos *Molothrus ater* ocasiona fracasos de nidificación en *Melospiza melodia*, una especie hospedera común. Cuando el número de *M. ater* hembras se redujo experimentalmente, los fracasos de nidificación se redujeron del 65.0% ( $n = 663$  nidos) al 49.9% ( $n = 331$ ). La reducción de parásitos disminuyó la frecuencia de fracasos de nidificación a un tercio de los niveles del grupo control de *M. melodia* durante los últimos 80 días de su temporada reproductiva, cuando ocurrió la mayoría de la ovoposición de los parásitos. La reducción de parásitos disminuyó considerablemente el fracaso de nidificación en nidos con huevos y donde había pollos. Las tasas diarias de fracaso fueron independientes de la presencia o ausencia de parasitismo en los nidos. Contrastamos dos hipótesis que explican como los parásitos causan el fracaso de nidificación en los hospederos: primero, la remoción de los huevos por parte de la hembra de *M. ater* conlleva a un tamaño de nidada inferior al límite que ocasiona la deserción del nido; segundo, los parásitos ocasionan el fracaso de nidificación porque destruyen la nidada, huevos o pollos, por completo. En apoyo a la primera hipótesis, se observó que la deserción posterior al parasitismo y remoción de huevos fue menos frecuente en nidos con menos parásitos (8.9%  $n = 158$  nidos) que en los controles sin manipulación (16.5%  $n = 424$  nidos). En apoyo a la segunda hipótesis, se observaron menos nidos con pollos muertos cuando el número de parásitos se redujo (2.5%  $n = 158$ ); en los controles hubo una mayor incidencia de muertes (4.7%  $n = 424$  nidos). En contraste, la proporción de nidos fracasados después de la desaparición de los huevos, pollos, o ambos, y después de la deserción en nidos sin parasitar, se incrementó con la reducción de los parásitos. Aunque nuestro estudio apoya ambas hipótesis, la deserción inducida

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por los parásitos tuvo una mayor contribución al fracaso de nidificación que la depredación por parásitos. Nuestro estudio sugiere que los programas de remoción de parásitos pueden beneficiar tanto a hospederos comunes como a hospederos amenazados al reducir las tasas de fracaso de nidificación.

THE BROOD PARASITIC Brown-headed Cowbird (*Molothrus ater*) reduces nesting success of its hosts in at least four ways. First, several host species routinely desert clutches after they are parasitized (e.g. McLaren and Sealy 2000, Budnik et al. 2001) or after a behavioral interaction with a female cowbird (e.g. Strausberger and Burhans 2001). Second, by removing eggs from host nests (Sealy 1992, Hill and Sealy 1994), cowbirds can reduce host clutch sizes below a desertion threshold (Rothstein 1982). Third, female cowbirds destroy host clutches and broods (review in Arcese et al. 1996, Granfors et al. 2001). Finally, competition between host and parasite nestlings for food can reduce host survival during the nestling phase (Chace et al. 2000). As a result, nests that are parasitized by cowbirds nearly always produce fewer host young than unparasitized nests (Payne and Payne 1998, review in Lorenzana and Sealy 1999).

The ecological significance of nest failures induced by cowbirds is not yet well established. Arcese et al. (1996) found local increases in rates of nest failure with higher frequencies of parasitism in Song Sparrows (*Melospiza melodia*), and Arcese and Smith (1999) showed that that result applies widely across the geographic range of the Song Sparrow. Wolf (1987) and Clotfelter and Yasukawa (1999) found similar results in Dark-eyed Juncos (*Junco hyemalis*), and Red-winged Blackbirds (*Agelaius phoeniceus*), respectively. In contrast, McLaren and Sealy (2000) found a negative association between parasitism and nest failure in Yellow Warblers (*Dendroica petechia*). Two recent video monitoring studies (Thompson et al. 1999, Granfors et al. 2001) have provided direct evidence of how often and by what means cowbirds lower host reproductive success. Both studies, however, were conducted at sites where cowbird parasitism was infrequent, and few nests failed because of the effects of cowbirds. Effects of cowbirds might differ when cowbirds are abundant relative to hosts and when more than one cowbird female visits each host nest (Trine 2000).

Cowbird removals are useful for exploring effects of parasitism (De Groot et al. 1999) and can provide insight into the mechanisms by which cowbirds reduce host reproductive success. Previous cowbird removals have mostly been part of management programs (Whitfield et al. 1999, Griffith and Griffith 2000, Hayden et al. 2000, Whitfield 2000; but see Stutchbury 1997) and have generally led to reduced levels of nest failure in hosts. Two of those studies involved planned experiments (Stutchbury 1997, Whitfield et al. 1999). Removal of a species from a predator community can improve the survival of prey species (e.g. Bayne and Hobson 2002) or leave it unchanged because of compensatory predation (e.g. Reitsma et al. 1990).

Smith et al. (2002) recently found that reducing cowbird numbers doubled annual reproductive success of Song Sparrows and reduced rates of daily nest failure by about one-third at each of two removal sites. In this companion article, how cowbird removal altered failures in Song Sparrow nests at those sites is explored in detail. The Song Sparrow is the most frequently used cowbird host at those riparian sites (our unpublished results). Two hypotheses were tested about the mechanisms by which cowbirds alter nest failure: (1) nest failures induced by cowbirds occur when hosts desert their clutches after cowbirds remove eggs (cowbird-induced desertion hypothesis; Rothstein 1982); (2) nest failure occurs when cowbirds remove or break all eggs or kill or remove all nestlings in a host's nest (cowbird predation hypothesis; Arcese et al. 1996, McLaren and Sealy 2000). The main prediction of the induced-desertion hypothesis is that cowbird reduction should result in fewer clutches being deserted after egg removal by cowbirds. Cowbirds routinely remove eggs from parasitized clutches (Lorenzana and Sealy 1999) and may also remove eggs from unparasitized clutches (Arcese and Smith 1999). The cowbird-predation hypothesis predicts that after cowbird reduction there should be fewer cases where (1) entire clutches or broods disappear from the nests, (2) young are killed in the nest but not eaten, or (3) young are dragged from the nest and left to die of exposure.

## METHODS

We worked at three riparian study sites in the Fraser River Delta (Westham, Delta, and Deas) from 1995 to 1999. Rogers et al. (1997) and Smith et al. (2002) describe the vegetation at the sites and general methods used. Sites differed to a moderate degree in sparrow density and cowbird feeding opportunities, both of which were highest at Westham (Smith et al. 2002). Female cowbirds were removed at Westham and Delta using two portable house traps set simultaneously ~1 km apart at each site (Smith et al. 2002). Only females were removed, because nearly all reports of cowbirds destroying or disturbing contents of host nests involve females (Arcese et al. 1996, Granfors et al. 2001; but see Sealy 1994). Fifty-one cowbirds were removed from Westham in 1996, 163 from Westham in 1997, and 24 from Delta in 1998. The third site, Deas, was not manipulated. Female cowbirds were held in captivity and released at the end of the breeding season. Removals progressively reduced cowbird parasitism during the breeding season but never eliminated it completely. Removals were most effective at Delta in 1998, and least effective at Westham in 1996 (Smith et al. 2002).

Other potential nest predators at the three sites included three species of garter snake (*Thamnophis* spp.), raccoon (*Procyon lotor*), mink (*Mustela vison*), eastern gray squirrel (*Sciurus carolinensis*), black rat (*Rattus rattus*), deer mouse (*Peromyscus maniculatus*), Northwestern Crow (*Corvus caurinus*) and Cooper's Hawk (*Accipiter cooperi*). Two additional predators, Douglas squirrel (*Tamiasciurus douglasii*) and Steller's Jay (*Cyanocitta stelleri*), were uncommon or absent at Westham and Deas but were seen regularly at Delta. A third, the Marsh Wren (*Cistothorus palustris*), was common at Westham and is a known egg predator there (Picman 1977), but it was rare at Delta and Deas.

In coastal British Columbia, the Song Sparrow typically lays an egg per day and incubates a clutch of 3–4 eggs for a median of 13 days. Incubation often begins on the day before the last egg is laid. The average duration of the nestling phase is 10–11 days. We assume here that the typical nesting cycle lasted 25 days (1 day laying + 13 days incubation + 11 days as a nestling). When a nest fails, relaying by the same female begins a mean of nine days later. The breeding season lasts ~120 days from late March to late July and individual females lay 1–6 clutches and rear 1–4 broods per year (Arcese et al. 2002, Smith et al. 2002).

Reproduction of Song Sparrows was studied at all sites in all five years (except at Deas in 1999). Focus here was on causes and timing of nest failure. Nest fate (success, failure, or outcome uncertain) was determined from (1) appearance of the clutch, brood, or nest on each check; (2) temperature (cold–warm) of eggs in the nest; (3) activity of parents (alarm calling, carrying food); and (4) presence and age of fledglings

near the nest. Nests that produced at least one sparrow or cowbird fledgling (or contained live nestlings >8 days old) were defined as successful. For 9% of nests, live nestlings >5 days old were observed on one check, the nest was empty on the next check, and it was not confirmed as successful by the presence of fledglings near the nest. The fate of those nests was defined as “uncertain.” Clutches were scored as deserted when eggs were cold and no parents were seen near the nest on two checks over at least three days. When desertion was only suspected after two checks, further checks were conducted until the status of the nest became clear.

To examine specific circumstances associated with nest failure, types of failure were divided into six categories. Definitions of those categories and their known or suspected relationships to cowbird reproductive activity are given in Table 1. Nests that were found while being built but were not finished were excluded from analysis. Also excluded here were 14 nests that failed for reasons other than nest predation (the nest was flooded, fell, or was stepped on by a cow; the clutch was infertile).

Effects of cowbird reduction on the frequency of nest failure at different times were estimated by calculating odds ratios and their associated confidence intervals (Sokal and Rohlf 1995) for each 20-day period of the sparrow's nesting season. An odds ratio provides a direct estimate of the proportional effect of an experimental treatment. For example, an odds ratio of 1.0 indicates the absence of an effect, whereas one of 3.0 indicates a threefold change because of the treatment. Odds ratios were calculated using procedure logistic in SAS (SAS Institute 1989).

Contingency table analyses were used to test for heterogeneity among all years and sites. A log-linear analysis was conducted to examine interactions among nest fate (failed or succeeded), treatment (control or cowbird reduction) and year (1996, 1997, 1998) ( $2 \times 2 \times 3$  multiway contingency table; Statsoft 1995). Data for 1996–1998 were used here, because simultaneous reduction and control data were available only for those three years. Daily nest survival rates and their standard errors were calculated separately for egg and nestling stages and for parasitized and unparasitized nests, using the method of Bart and Robson (1982) and the program in Krebs (1999). Daily nest survival rates were compared among sites and treatments using the program CONTRAST (Sauer and Williams 1989). Log-likelihood ratio tests were used to test how specific types of failure responded to treatment. We did that by comparing proportions of each failure type between control and cowbird reduction treatments to the pooled proportion of the five remaining types across the two treatments. Because six independent comparisons were conducted here, alpha was adjusted from 0.05 to 0.008. Finally, for nests where the timing of failure could be established,

TABLE 1. Types of nest failure, their definitions, and prior reasons for connecting them to activity of Brown-headed Cowbirds at host nests.

Type	Definition	Connection with Brown-headed Cowbird activity
Complete failure	No intact eggs or young remain in the nest	Typical case of nest predation expected for predators other than cowbirds. Cowbirds, however, can remove all eggs or young from a host nest (e.g. Granfors et al. 2001).
Unparasitized and deserted	Unparasitized clutch deserted, often after a prior reduction in size	Cowbirds may remove eggs from unparasitized clutches (Arcese and Smith 1999). Behavioral interactions between hosts and brood parasites may cause hosts to desert (Arcese et al. 1996).
Parasitized and deserted	A parasitized clutch was reduced in size and deserted	Cowbirds frequently remove eggs from parasitized nests (Lorenzana and Sealy 1999). Reductions in clutch size can induce desertion by hosts (Rothstein 1982).
Dead-injured nestlings	Nestlings found dead or injured in nest, or dead near-below the nest	Cowbirds are known to attack and injure or kill host young, or to drag them from the nest (e.g. Arcese et al. 1996, Granfors et al. 2001).
Nestlings gone, eggs remain	All young gone from nest; intact eggs remain	Cowbirds might drag host young from nest (e.g. Granfors et al. 2001), but leave unhatched eggs in the nest.
Other	Various circumstances	Mainly nests that were found empty, often with parents in attendance, but which never contained eggs or young. Also includes cases of young starved or female killed on the nest.

the time of nest failure was classified into four categories: (1) the nest failed during laying or in the first half of the 13-day incubation period, (2) it failed during the second half of the incubation period, (3) it failed early during the nestling phase (nestlings 0–5 days old), and (4) it failed late during the nestling period (nestlings >5 days old).

## RESULTS

*Cowbird reduction and overall pattern of nest failure.*—Specific fates of 663 control nests over five years were determined as well as 331 nests in the three removal years. Of those 994 nests, 312 successfully reared nestlings of either species, 86 were of uncertain status, and 596 failed (Appendix). Focus here was mainly on the 596 failures. Proportions of control nests in those three categories (success, failure, or uncertain) did not differ significantly by either site or year (contingency table analyses, all  $P > 0.05$ ). Therefore samples were pooled across sites and years within treatments for further analyses.

The frequency of parasitism by cowbirds varied through the sparrow's breeding season, rising to a peak in early June (Fig. 1A) and then declining. Number of cowbird eggs laid per parasitized nest also rose as the season progressed but did not decline late in the season (Fig. 1B). The odds-ratio analysis (Fig. 1C) revealed that cowbird reduction lowered nest failure rates

by more than 2-fold (overall odds ratio = 2.08, 95% confidence intervals 1.54–2.81). There was little cowbird trapping during the first two 20-day intervals (up to 10 May, Fig. 1); therefore, there was no treatment effect up to May 10. In those periods, cowbirds were beginning to breed, and multiple parasitism was rare (Fig 1B). From 11 May on, however, cowbird activity in controls increased to a much higher level. Over 55% of nests were parasitized (Fig. 1A), 1.36–1.71 cowbird eggs were laid per parasitized nest (Fig. 1B), and more cowbirds were trapped. After 10 May, cowbird trapping reduced the proportion of nests that failed significantly in two of the four 20-day periods, and the reduction approached significance in a third (after 8 July). Strong effects were seen from 11 May to 30 May and from 20 June to 9 July (both  $P < 0.001$ ,  $df = 1$ , maximum-likelihood chi-square tests,  $\chi^2 = 19.48$  and  $12.84$ , respectively). Absence of an effect between 31 May and 19 June was due to higher frequencies of nest failure in the cowbird reduction treatment (0.53) than in the other three periods after 10 May (0.38–0.43).

We used a log-linear analysis to test for interactions between nest fate (success–fail), treatment (cowbird reduction–control), and year (1996, 1997, 1998) for the three removal years (Table 2). Significant two-way interactions were found ( $\chi^2 = 72.6$ ,  $df = 5$ ,  $P < 0.001$ ) but no

TABLE 2. Effects of cowbird reduction on numbers of Song Sparrow nests that failed, succeeded, or were of uncertain fate. Numbers in parentheses are percentages of nests in each category. The right-hand column is a chi-square value ( $df = 1$ ) comparing the proportions of successes and failures between controls and removals in each period.

Treatment	Number of nests failing (%)	Number of nests succeeding (%)	Fate uncertain (%)	$\chi^2$
1995 Control	46 (62)	18 (24)	10 (14)	–
1996 Control	37 (63)	14 (24)	8 (14)	0.91 ( $P > 0.25$ )
1996 Removal	51 (56)	28 (31)	12 (13)	
1997 Control	81 (63)	40 (31)	8 (6)	6.5 ( $P < 0.015$ )
1997 Removal	67 (46)	64 (44)	14 (10)	
1998 Control	145 (59)	82 (33)	18 (7)	2.2 ( $P > 0.10$ )
1998 Removal	47 (49)	39 (41)	9 (6)	
1999 Control	110 (68)	42 (26)	9 (6)	–
All control	431 (65)	181 (27)	51 (8)	21.2 ( $P < 0.001$ )
All removals	165 (50)	131 (40)	35 (11)	

three-way interaction ( $\chi^2 = 0.5$ ,  $df = 2$ ,  $P = 0.785$ ). Nest fate was dependent on treatment (marginal  $\chi^2 = 13.6$ ,  $df = 1$ ,  $P = 0.002$ ; partial  $\chi^2 = 13.3$ ,  $df = 1$ ,  $P < 0.001$ ). Sparrow nests were more likely to fail in the control (63% of 440 nests) than in the reduction treatment (52% of 252 nests). A second two-way interaction was found between treatment and year (marginal  $\chi^2 = 55.2$ ,  $df = 2$ ,  $P < 0.001$ ; partial  $\chi^2 = 54.9$ ,  $df = 2$ ,  $P < 0.001$ ). Compared to the controls, a greater proportion of nests was found in the cowbird reduction treatment in 1996 (60.8% of 130 nests) and 1997 (52.0% of 252 nests) but a lower proportion in 1998 (27.7% of 310 nests). The latter interaction arose because we always found more nests each year at Westham, which was the removal site in 1996 and 1997 and the control site in 1998. More sparrow territories were monitored at Westham, and nesting there began slightly earlier each year than at the other two sites (Smith et al. 2002).

*Cowbird reduction and type of nest failure.*—Proportions of the six types of nest failure did not vary significantly across control sites or years, or between removal sites (contingency table analyses, all  $P > 0.10$ ). Although there was variation in number of nests found at different times across sites (see above), there were no significant shifts in failure type between early and late nests at the same site (contingency table analyses,  $P > 0.10$ ). Therefore data were pooled for further analyses.

Overall distribution of failure types shifted significantly after cowbird reduction ( $\chi^2 = 15.04$ ,  $df = 5$ ,  $P < 0.01$ ; Table 3). When significant

reductions for particular types of failure were looked for, however, no single type differed significantly ( $P < 0.008$ ) among treatments after Bonferroni correction (Table 3). After cowbird reduction, the percentage of parasitized and deserted nests fell from 16.5% in controls to 8.9%. Failures involving dead or injured nestlings also decreased in frequency from 4.7 to 2.5% after cowbird numbers were reduced. Failures when nestlings disappeared but eggs were left in the nest decreased from 6.1 to 2.5%. Complete failures increased from 45.3 to 57% after cowbird reduction and failures involving unparasitized and deserted nests increased from 6.6 to 10.8%. Failures from other causes remained unchanged after cowbird reduction (Table 3).

*Cowbird reduction and timing of failure within the nesting cycle.*—Daily nest survival was markedly lower during the egg stage of the nesting cycle than during the nestling stage. On average, 5.2% of control nests failed per day at the egg stage, compared to 3.4% per day at the nestling stage (CONTRAST,  $\chi^2 = 12.88$ ,  $df = 1$ ,  $P < 0.001$ ; Table 3). Cowbird reduction decreased daily survival rates consistently across sites at the egg stage at both Westham and Delta (Table 4) and that difference was significant at each site ( $\chi^2 = 4.43$ ,  $df = 1$ ,  $P = 0.04$  at Westham;  $\chi^2 = 5.82$ ,  $df = 1$ ,  $P = 0.02$  at Delta), and in pooled data for both sites ( $\chi^2 = 9.09$ ,  $df = 1$ ,  $P = 0.003$ ). Survival over the whole egg stage was improved from 0.47 to 0.61. At the nestling stage, removals again decreased daily failure rates by 0.4 to 0.8% and survival over the whole nestling period im-

proved from 0.68 to 0.75. However, treatment effects in the nestling stage were not significant at Westham ( $\chi^2 = 1.45$ ,  $df = 1$ ,  $P = 0.23$ ), Delta ( $\chi^2 = 0.19$ ,  $df = 1$ ,  $P = 0.66$ ), or for both sites pooled ( $\chi^2 = 3.25$ ,  $df = 1$ ,  $P = 0.07$ ). In cowbird reduction treatments, survival was no longer significantly higher at the nestling stage than the egg stage ( $\chi^2 = 2.46$ ,  $df = 1$ ,  $P = 0.12$ ).

The nesting cycle was next divided into four periods (laying and early incubation, late incubation, early nestling, and late nestling) to test for finer temporal differences in effects of removal on nest failure. In those comparisons, cowbird reductions did not alter the timing of nest failures significantly (contingency table analyses, all  $P > 0.05$ ).

*Survival of parasitized versus unparasitized nests.*—Individual cowbird females have been hypothesized to destroy host breeding attempts to enhance their future laying opportunities. That hypothesis predicts that, when individual cowbirds can monopolize groups of host nests, parasitized nests should fail at lower rates than unparasitized nests (Arcese et al. 1996, Hauber 2000). If, however, female cowbirds have overlapping laying areas, the reverse prediction should apply (Arcese et al. 1996). The frequent multiple parasitism at our sites (see below) suggests that the second prediction is more appropriate here. However, daily survival rates in parasitized and unparasitized nests were found to be very similar in both control and cowbird reduction treatments (Table 5).

#### DISCUSSION

*Effects of cowbird reduction on nest failure.*—Our study was designed to explore timing and causes of nest failure in Song Sparrows and to

test experimentally if and when cowbirds contribute to nest failures in that host species. The frequency of nest failure was not affected by reductions in cowbird numbers before 10 May, when parasitic activity by cowbirds was low (Fig. 1A, B) and cowbird trapping was just becoming effective. After 10 May, however, cowbird trapping reduced the average frequency of nest failure by nearly 3-fold (Fig. 1C). Rates of daily nest failure at the egg stage were reduced strongly by cowbird reduction (Table 4). There was also a weaker trend for daily failure rates to be reduced at the nestling stage. Our experiment confirms several descriptive studies reporting that cowbirds cause or facilitate nest failures in Song Sparrows (Arcese et al. 1992, 1996; Smith and Arcese 1994; Arcese and Smith 1999; Hauber 2000) and other species (Wolf 1987, Clotfelter and Yasukawa 1999).

To account for mechanisms behind that result, two hypotheses were tested: the cowbird-induced nest-desertion hypothesis, where nests are deserted after cowbirds remove eggs and add fewer parasitic eggs; and the cowbird predation hypothesis, where nest failure occurs when cowbirds remove or break all eggs or kill or remove all nestlings in a host's nest.

*The cowbird-induced desertion hypothesis.*—In agreement with that hypothesis, cowbird reduction lowered nest failure rates most strongly at the egg stage (Table 3). Also, frequency of desertion after parasitism fell from 16.5% in controls to 8.9% after cowbird reduction (Table 3). Rogers et al. (1997) noted a higher frequency of desertion and parasitism (26% of 346 failing nests) at Westham in 1988–1991. At that time, parasitism was more intense (2.0 cowbird eggs per parasitized nest) than in our

TABLE 3. Effects of reducing numbers of female cowbirds on categories of nest failure in Song Sparrows.

Definitions of failure types are given in Table 1. G values for rows 1–6 are from a  $2 \times 2$  test of independence contrasting numbers of controls versus removals for each type versus numbers for all remaining failures for other types (with Williams' correction). The bottom right value is from a chi-square test ( $df = 5$ ) on the  $2 \times 6$  table of all six types.

Failure type	Number in controls (%)	Number in removals (%)	G statistic (P value)
Complete failure	192 (45.3)	90 (57.0)	6.3 (<0.02)
Unparasitized and deserted	28 (6.6)	17 (10.8)	2.6 (>0.1)
Parasitized and deserted	70 (16.5)	14 (8.9)	5.9 (<0.02)
Dead-injured nestlings	20 (4.7)	4 (2.5)	1.5 (>0.1)
Nestlings gone, eggs remain	26 (6.1)	4 (2.5)	3.4 (<0.1)
Other	88 (20.8)	29 (18.4)	0.4 (>0.5)
Total	424	158	15.0 (<0.01)

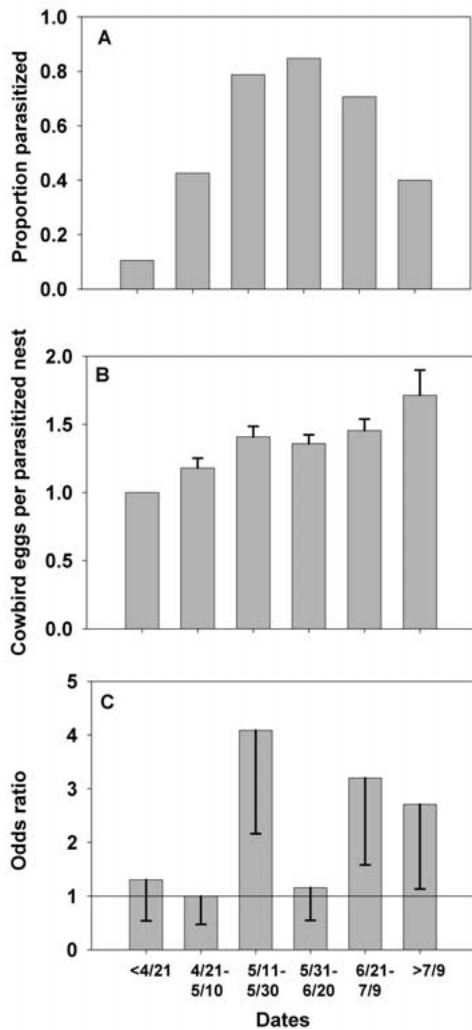


FIG. 1. (A) Proportions of all control nests per period containing one or more cowbird eggs or young for six 20-day periods during the Song Sparrow breeding season; (B) mean number of cowbird eggs per parasitized control nest ( $\pm$ SE) for the same six periods; (C) odds ratios comparing controls and the cowbird reduction treatments for each 20-day period. Vertical bars are the lower 95% confidence intervals. The horizontal line (odds ratio = 1.0) indicates the absence of a treatment effect. An odds ratio with the lower confidence bound  $>1$  indicates a significant treatment effect. Upper confidence bounds are not displayed because only the lower bounds are of interest here.

study (1.4 cowbird eggs per parasitized control nest). Cowbirds also remove eggs from unparasitized clutches (Arcese and Smith 1999), but that was not a dominant cause of nest failure in

our study because the frequency of unparasitized and deserted nest failures increased after cowbird reduction (Table 3).

The best current way to assess causes of failure is to record predators at the nest on videotape. In the most extensive video monitoring study conducted to date, Granfors et al. (2001) documented eight cases of disturbance by female cowbirds in 132 nests of a variety of host species. Six of those cases involved partial removal of eggs, and in three of those cases the host abandoned the nest. Cowbird parasitism in Granfors et al.'s study, however, was only about one-fifth as frequent as it was at our sites. Without video records, whether egg removal alone was sufficient to cause nest failure or whether egg removal plus a struggle with a female cowbird was involved could not be assessed.

Our data thus support the cowbird-induced desertion hypothesis. Increased desertion was the only type of failure restricted to the egg stage that was reduced after cowbird reduction, and the egg stage was where most of the improvement in daily nest survival occurred after reduction (Table 4).

*The nest-predation hypothesis.*—That hypothesis predicts declines in clutch-brood destruction after cowbird reduction at both egg and nestling stages. A decrease in complete failures was not found. In fact, frequency of complete failures increased from 45.3 to 57.0% after cowbird reduction (Table 2). The simplest explanation for that result is that other nest predators caused most complete failures, and that relative frequency of failures caused by those predators increased as effects of cowbird-induced failures were reduced. In support of that explanation, in the video monitoring studies by Thompson et al. (1999) and Granfors et al. (2001), none of eight cases of cowbird disturbance to nests involved complete removal of all eggs or young. One of our results, however, suggested that cowbird predation did contribute to failures at the nestling stage. When we removed cowbirds, failures when nestlings were killed, injured, or dragged from the nest became less frequent, which suggests that cowbirds killed some broods by injuring young in the nest, removing young from the nest, or both. In their video monitoring studies, Granfors et al. (2001) documented two fatal attacks on host nestlings in 132 nests and Thompson et al. (1999) documented one nonfatal attack in a sample of 52 nests. Arcese

TABLE 4. Daily nest survival rates ( $\pm 1$  SE) and cumulative overall survival of Song Sparrow nests in egg stage, nestling stage, and over both stages combined in relation to treatment (control vs. cowbird reduction). Control data from 1995 to 1999, cowbird reduction data from 1996 to 1998.

Treatment	Site	Daily survival rate ( $\pm 1$ SE) egg stage	Survival for 14 days egg stage	Daily survival rate ( $\pm 1$ SE) nestling stage	Survival for 11 days nestling stage	Survival for 25 days both stages
Control	Westham	0.949 $\pm$ 0.006	0.479	0.968 $\pm$ 0.004	0.697	0.336
	Delta	0.940 $\pm$ 0.007	0.532	0.967 $\pm$ 0.006	0.645	0.290
	Deas	0.956 $\pm$ 0.007	0.418	0.961 $\pm$ 0.006	0.689	0.344
	All	0.947 $\pm$ 0.004	0.473	0.966 $\pm$ 0.003	0.680	0.319
Cowbird reduction	Westham	0.965 $\pm$ 0.005	0.609	0.975 $\pm$ 0.004	0.756	0.460
	Delta	0.965 $\pm$ 0.008	0.609	0.971 $\pm$ 0.007	0.722	0.439
	Both	0.965 $\pm$ 0.004	0.609	0.974 $\pm$ 0.003	0.747	0.455

et al. (1996) also compiled several anecdotal accounts of fatal attacks by cowbirds. However, although cowbirds are known to kill and injure host young and remove them from nests, other nest predators might also cause such failures.

Brown-headed Cowbirds may prey upon host nests as a tactic to increase their reproductive success (Arcese et al. 1996). A cowbird may locate a host nest at a stage of the nesting cycle inappropriate for parasitic egg-laying (e.g. late in incubation). By destroying that nest, the cowbird may encourage renesting thereby giving the cowbird a future opportunity for successful parasitism. If that were the case, destruction of nests should cease near the end of the breeding season when any benefits of inducing hosts to renest approach zero. In agreement with that suggestion, both overall nest failure rate and frequency of failures involving killing or removal of host young from the nest did decrease late in the season. Overall failure rates in control nests fell by one-third after 30 June and there were no cases where nestlings were killed in or near the nest after 23 June. In contrast,

failures when nestlings were removed, leaving only eggs (which also decreased after cowbird reduction; Table 3), peaked in frequency near the end of the breeding season when frequency of parasitism was declining (Fig. 1A). We therefore doubt that that last type of failure is associated with cowbirds.

Destruction of host clutches and broods is practiced by other species of brood parasites. Shiny Cowbirds (*Molothrus bonariensis*) frequently puncture host eggs causing clutches to fail (Nakamura and Cruz 2000). Egg puncture in Shiny Cowbirds can reflect intense competition among parasite females for hosts (Davies 2000) and may provide information to a female Shiny Cowbird about whether a clutch is suitable for parasitic laying (Massoni and Reboreda 1999). Great Spotted Cuckoos (*Clamator glandarius*) may depredate Eurasian Magpie (*Pica pica*) nests, if the magpies eject the mimetic cuckoo egg (Soler et al. 1995).

A plausible alternative explanation for shifts in frequency of failure after cowbird reduction is that cowbirds were responsible for failures in

TABLE 5. Daily nest survival rates ( $\pm 1$  SE) and overall survival probabilities of Song Sparrow nests in relation to cowbird parasitism and cowbird reduction.

Treatment	Site	Parasitized nests		Unparasitized nests	
		Daily survival rate ( $\pm 1$ SE)	Probability of nest success over 25 days	Daily survival rate ( $\pm 1$ SE)	Probability of nest success over 25 days
Control	Westham	0.954 $\pm$ 0.004	0.313	0.952 $\pm$ 0.008	0.291
	Delta	0.958 $\pm$ 0.006	0.342	0.946 $\pm$ 0.008	0.249
	Deas	0.956 $\pm$ 0.006	0.326	0.967 $\pm$ 0.007	0.436
	All	0.956 $\pm$ 0.003	0.322	0.954 $\pm$ 0.005	0.310
Cowbird reduction	Westham	0.971 $\pm$ 0.006	0.481	0.972 $\pm$ 0.004	0.496
	Delta	0.973 $\pm$ 0.009	0.510	0.963 $\pm$ 0.006	0.394
	Both	0.973 $\pm$ 0.005	0.499	0.970 $\pm$ 0.004	0.461

categories that both increased and those that decreased after cowbird reduction. If that was the case, categories that increased in frequency (e.g. complete failure) would have done so because cowbirds caused relatively fewer failures of that type than in categories that decreased in frequency.

We suggest that cowbirds cause nest failures in Song Sparrows both by removing eggs from nests so that a desertion threshold is met (Rothstein 1982, Hill and Sealy 1994), and by depredating nests containing young. We have not shown that cowbirds do not cause complete failures or desertion of unparasitized nests, but only that those types of failures are uncommon relative to desertion after parasitism and egg removal. Declines in failures owing to desertion of parasitized nests here and strong reductions in daily failure rate at the egg stage suggest that desertion was the dominant cause of failure in our study.

In contrast, Arcese et al. (1996) argued that predation of eggs and young by cowbirds was the dominant mechanism for nest failure in Song Sparrows on nearby Mandarte Island. They did not, however, examine the role of desertion. Differences in mechanisms by which cowbirds cause nest failure between Mandarte and at our sites are quite plausible, because the sites differ in several respects. On our sites, cowbirds are much more abundant, multiple parasitism is more common, and interference between cowbird females may be more important. Also, frequent tall trees at our sites provided numerous perches, which cowbirds can use to search for nests. Cowbirds may therefore have used different reproductive tactics in the two different areas (see also Arcese et al. 1996). Although our results suggest that cowbirds cause nest failures directly, failures might also occur indirectly if cowbirds drew the attention of other predators to the nest location (Arcese et al. 1996). Such failures would be difficult to detect, even with video evidence from the nest site.

Cowbird removals are used in management of several endangered species of songbird (Rothstein and Cook 2000). Three of those programs (Whitfield et al. 1999, Griffith and Griffith 2000, Hayden et al. 2000, Whitfield 2000) found that cowbird removal lowered nest failure rates in the endangered hosts. Two descriptive studies (Wolf 1987, Clotfelter and Yasukawa 1999) also provide support for that idea. In contrast,

one other removal study (Stutchbury 1997) and one descriptive study (McLaren and Sealy 2000) did not find evidence that cowbirds cause nest failures. Fates of cowbird eggs can differ strongly in nests of different hosts (Scott and Lemon 1996) and between different populations of the same host (Smith and Arcese 1994, Rogers et al. 1997), so those differences are not surprising.

Predator removals to manage game birds (reviewed in Newton 1998) and to investigate nest predation (e.g. Reitsma et al. 1990) have often been unsuccessful because of compensatory predation. In those cases, other predator species increased their effects on a target species when one predator was removed. Effects of such predator manipulations may also vary if decreasing densities of the principal predator has a positive influence on densities of other potential predators within the community (Schmidt et al. 2001). However, it seems that habitat managers who wish to protect endangered species by reducing the predatory effects of cowbirds need not be too concerned about compensatory changes in mortality. Reducing cowbird abundance generally seems to increase nest survival in commonly used cowbird hosts, probably because cowbirds are frequently a dominant cause of nest failure in such hosts. Further experimental and descriptive studies of the magnitudes and causes of cowbird-induced nest failure, however, are needed. Such studies could usefully employ detailed video monitoring of the causes of nest failure in large samples of nests (Thompson et al. 1999, Granfors et al. 2001).

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APPENDIX. Cases of nest success and failure type by site and year. WE = Westham, DL = Delta and DE = Deas. For definitions of failure types, see Table 1.

Failure type	WE 95	WE 96	WE 97	WE 98	WE 99	DL95	DL 96	DL 97	DL 98	DL 99	DS95	DS 96	DS 97	DS 98	Total
Complete	18	26	41	46	28	2	12	21	23	18	1	4	17	25	282
Unparasitized, deserted	2	2	6	8	2	1	1	7	9	2	0	0	1	4	45
Parasitized, deserted	8	7	2	12	10	2	5	10	5	5	1	3	5	9	84
Nestlings killed or injured	2	1	3	2	5	0	0	3	0	4	0	2	0	2	24
Nestlings gone, eggs remain	2	1	2	4	6	0	1	2	1	3	0	0	0	8	30
Other	3	13	9	26	20	2	4	3	7	6	2	2	10	10	117
Nonpredation	0	1	4	0	0	0	2	2	2	1	0	1	0	1	14
All failures	35	51	67	98	71	7	25	48	47	39	4	12	33	59	596
Successes	15	28	64	43	30	2	8	19	39	12	1	6	21	24	312
Uncertain	4	12	14	9	3	4	7	5	9	6	2	1	3	7	86
Total	54	91	145	150	104	13	40	72	95	57	7	19	57	90	994