

COWBIRD REMOVALS UNEXPECTEDLY INCREASE PRODUCTIVITY OF A BROOD PARASITE AND THE SONGBIRD HOST

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Abstract. Generalist brood parasites reduce productivity and population growth of avian hosts and have been implicated in population declines of several songbirds of conservation concern. To estimate the demographic effects of brood parasitism on Bell's Vireos (*Vireo bellii*), we removed Brown-headed Cowbirds (*Molothrus ater*) in a replicated switchback experimental design. Cowbird removals decreased parasitism frequency from 77% and 85% at unmanipulated plots to 58% and 47% at removal plots in 2004 and 2005, respectively. Vireo productivity per pair was higher at cowbird removal plots when years were pooled (mean = 2.6 ± 0.2 [SE] young per pair) compared to unmanipulated plots (1.2 ± 0.1). Nest desertion frequency was lower at cowbird removal plots (35% of parasitized nests) compared to unmanipulated plots (69%) because removal of host eggs was the proximate cue for nest desertion, and vireos experienced lower rates of egg loss at cowbird removal plots. Nest success was higher among unparasitized than parasitized nests, and parasitized nests at cowbird removal plots had a higher probability of success than parasitized nests at unmanipulated plots. Unexpectedly, cowbird productivity from vireo pairs was higher at cowbird removal plots (mean = 0.3 ± 0.06 young per pair) than at unmanipulated plots (0.1 ± 0.03) because fewer parasitized nests were deserted and the probability of nest success was higher. Our study provides the first evidence that increases in cowbird productivity may be an unintended consequence of cowbird control programs, especially during the initial years of trapping when parasitism may only be moderately reduced. Thus, understanding the demographic impacts of cowbird removals requires an informed understanding of the behavioral ecology of host–parasite interactions.

Key words: Bell's Vireo; brood parasitism; cowbird removal; *Molothrus ater*; productivity; seasonal fecundity; *Vireo bellii*.

INTRODUCTION

Successful conservation and management of threatened or endangered species depends on the identification of environmental factors that limit productivity or survival. In North America, brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") can reduce the productivity of songbird hosts, and cowbird parasitism has been implicated in the declines of several threatened or endangered songbirds. Several state and federal agencies have established large-scale cowbird removal programs to rescue declining host populations from the effects of parasitism. Some songbird species including Kirtland's Warbler (*Dendroica kirtlandii*), Least Bell's Vireo (*Vireo bellii pusillus*), and Black-capped Vireo (*Vireo atricapilla*) have benefited from cowbird removals, but it is difficult to determine if continued trapping is necessary to ensure that host population growth meets management objectives because host productivity is not regularly monitored at control areas. Nevertheless, cowbird trapping is often

applied as a conservation strategy, and traps are operated by private citizens in some areas where few host productivity data exist. Several researchers have suggested that removals should be discontinued in some areas to better understand how suspension of trapping affects hosts and that some funds be redirected to habitat conservation and restoration. Alternatively, experiments with replicated control and removal plots may help elucidate how parasitism limits host productivity and better guide management decisions regarding cowbird trapping. In this paper, we demonstrate that cowbird removals can increase the productivity of the nominate race of Bell's Vireo (*V. b. bellii*), which may be of benefit to the federally endangered Least Bell's Vireo and other small-bodied songbirds. However, we also demonstrate that cowbird removals can unexpectedly increase cowbird productivity from vireo nests, an undesirable result for managers wishing to reduce impacts of brood parasites.

The effects of interspecific brood parasitism on productivity differ among avian parasites and their hosts. European Cuckoos (*Cuculus canorus*) and honeyguides (Family Indicatoridae) are host specialists that cause complete reproductive failure because the parasitic young eject host eggs or nestlings, and kill host nest mates (Friedmann 1955, Davies and Brooke 1989).

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Despite a high cost of parasitism, cuckoos, honeyguides, and other host-specific brood parasites may have little population-level effects on host species because these parasites occur at low densities. In contrast, generalist brood parasites such as the Brown-headed Cowbird routinely parasitize a large number of host species and often occur at high densities (Robinson et al. 1995). Therefore, parasitism by cowbirds may have larger effects on the population viability of hosts than parasitism by cuckoos because cowbirds do not rely on a single host species to rear their young (Davies 2000).

Brood parasitism by cowbirds can reduce host productivity in several ways. The presence of cowbird eggs or nestlings can reduce hatchability of host eggs due to egg capping and reductions in incubation efficiency (Hauber 2003a, Hoover 2003). Cowbird eggs often hatch in a shorter period than host eggs, which confers a competitive advantage to parasitic young because they may be larger and more competitive in acquiring food than host nestlings (Lichtenstein and Sealy 1998, Kilner et al. 2004). Female cowbirds may directly reduce host productivity by removing host eggs prior to or following parasitism (Sealy 1992), and may destroy the contents of nests during incubation or brood-rearing to induce hosts to renest ("cowbird predation hypothesis"; Arcese et al. 1996, Granfors et al. 2001, Hoover and Robinson 2007). However, the fitness impacts of egg removal and nest destruction on host productivity may vary among and within cowbird populations (McLaren and Sealy 2000, Peer 2006). Species-specific costs of parasitism may also be influenced by the life history traits of host species; small-bodied species that have long incubation periods (>12 days) suffer the highest fitness costs (Hauber 2003b).

Reduced productivity due to cowbird parasitism has been implicated in population declines of several species of migrant songbirds in North America, and cowbird control has been implemented for at least four songbird species of conservation concern (Robinson et al. 1995). The effects of cowbird removals on host productivity can be difficult to evaluate because some applied studies were constrained by management objectives and did not monitor host productivity in reference areas where cowbirds were not removed (Griffith and Griffith 2000). In addition, combinations of several simultaneous management interventions such as cowbird removal, addling of cowbird eggs, and reduced cattle density may complicate the assessment of the effects of cowbird removals alone (Whitfield 2000, Kostecke et al. 2005). The use of long-term or open-ended cowbird trapping to aid in the recovery of songbird species has been questioned because control programs may direct funds away from habitat restoration, have rarely been discontinued, kill thousands of cowbirds annually, and may contribute to ongoing population declines in cowbirds (−1.2% per year; Rothstein and Peer 2005, Sauer et al. 2005).

Although primarily a management tool, cowbird removals have also been used in an experimental context to examine the effects of cowbird parasitism on host productivity, nest failure, and host community composition. At least seven field studies have examined the effects of cowbird removals on songbird population demography. Three studies lacked unmanipulated reference sites and cannot account for the effect of removals within a year (DeCapita 2000, Kostecke et al. 2005, Kus and Whitfield 2005). However, all of these studies were conducted on endangered species and provide valuable information regarding the trends of parasitism and productivity over time. Two studies had reference sites, but one added cowbird eggs in control and cowbird removal areas, making assessment of cowbird removals alone difficult (Whitfield 2000, Morrison and Averill-Murray 2002). One of the best designed studies examined the effects of cowbird removals on the demography of Song Sparrow (*Melospiza melodia*; Smith et al. 2002, 2003). However, Song Sparrows are a large-bodied host capable of rearing mixed broods containing both host and cowbird young. Experimental studies of the effects of cowbird control on small-bodied hosts are more relevant to the management of species of conservation concern. Moreover, spatial and temporal variation in cowbird densities and parasitism rates often occur at a regional scale, and removal experiments are needed to determine how these factors interact to influence the regional costs of parasitism for songbird hosts (Jensen and Cully 2005). In this study, we conducted a cowbird removal experiment in an area with high parasitism frequencies (>80% of nests for many host species) to evaluate the effects of cowbird parasitism and cowbird control on the productivity of a Great Plains population of Bell's Vireo (hereafter "vireo").

Our objective was to determine if parasitism by cowbirds can limit the productivity of a small-bodied songbird. We made four predictions. First, nest desertion by small-bodied hosts can reduce the costs of parasitism, and Parker (1999) found that 75% ($n = 44$) of the parasitized vireo nests were deserted at our study site. We expected that more instances of vireo egg removal by cowbirds would occur at higher cowbird densities because the potential for a nest to be discovered by multiple cowbirds would be greater. Thus, we predicted that desertion of parasitized nests would be less likely at removal plots because more vireo eggs would remain in parasitized nests at the end of the vireo egg-laying period. Second, cowbird abundance and vireo productivity could be negatively correlated if female cowbirds destroy vireo nests to induce renesting. However, at high cowbird densities, female laying ranges overlap and parasitized nests are predicted to fail more frequently than unparasitized nests (Arcese et al. 1996). If cowbirds destroy nests or facilitate nest failure at our study site, then the probability of nest success for parasitized nests would be lower than that for unpara-

sitized nests. We also predicted that parasitized nests at unmanipulated plots should have a lower probability of success than parasitized nests at removal plots. Third, higher cowbird density is associated with greater frequency of parasitism of vireo nests, and in turn, lower vireo productivity (Kus and Whitfield 2005). If these correlations represent causal mechanisms, we predicted that vireo nests would be parasitized less frequently, and show higher productivity per nest and higher seasonal fecundity at cowbird removal plots. Last, we expected cowbird density and productivity to be positively correlated, and predicted that cowbird productivity from vireo nests would be higher at plots where cowbirds were not removed.

METHODS

Study site and cowbird removal

Our study was conducted from 2003 to 2005 at the 3487-ha Konza Prairie Biological Station (hereafter "Konza") in the Flint Hills region of northeastern Kansas (39°05' N, 96°35' W). Konza is subdivided into ~60 experimental plots, and each plot receives a combination of fire and grazing treatments. Fire frequencies range from annual burning to 20-year burn intervals, and grazing treatments include cattle (*Bos taurus*), bison (*Bos bison*), and ungrazed plots. Native warm season grasses (e.g., big bluestem, *Andropogon gerardii*) are the dominant vegetation on the landscape, but woody shrubs including rough-leaved dogwood (*Cornus drummondii*), American plum (*Prunus americana*), and smooth sumac (*Rhus glabra*) become established when fire is excluded for at least four years (Hartnett et al. 1996, Briggs et al. 2002, 2005).

We selected five ungrazed and infrequently burned plots (KP1, KP2, KP3, KP4, KP5) that were heavily shrub-encroached, and studied the reproductive success of Bell's Vireos breeding within the plot boundaries (see Kosciuch [2006] for locations of plots at Konza). Study plots ranged from 24 to 83 ha in size. In 2004 and 2005, cowbird removals were conducted at two of five plots. In removal plots, three large drop-in cowbird traps (1.8 × 1.5 × 1.8 m) were placed around the perimeter of the plot at a density of one trap per 11 ha. In unmanipulated plots, no trapping was conducted. Cowbird removals were conducted in a replicated, switchback design. Cowbird traps located at KP1 and KP2 in 2004 were moved to KP3 and KP4 in 2005. No removals were conducted in 2003, and plot KP5 remained an unmanipulated reference plot in all three years.

Traps were operated from the first week in May to mid-July in each year (~70 trapping days). Each trap was initially stocked with several live decoy cowbirds, and food and water were provided ad libitum throughout the season. Traps were checked daily to record the number and sex of cowbirds captured and to release any nontarget species. Surplus cowbirds were removed from traps with handheld nets and euthanized by cervical dislocation when traps contained >20 individuals.

Vireo reproduction and response to parasitism

Bell's Vireos are an obligate shrub-nesting species that have well-defined territories at Konza (Parker 1999, Kosciuch et al. 2006). We visited territories every three days beginning with the arrival of the first males during the second week of May and ended our monitoring when the last broods fledged in early August. Territories were searched between 06:00 and 13:00 (Central Standard Time) to locate males and nests and to determine the stage of the nesting cycle. Nests were located by searching shrubs in the vicinity of singing males. We used song playbacks to verify the presence of males that were not singing when we entered their territory. We monitored between 52 and 62 pairs of vireos each year, and 10–30% of the males were uniquely color-banded each year. No color-banded male switched territories within a season. Bell's Vireos rarely switch mates within a season, but may divorce and remate between years (Budnik et al. 2000). The well-defined territories, easily located nests, and intensive nest monitoring enabled us to monitor the productivity of a large sample of vireo pairs throughout the breeding season.

Male vireos assist females in most aspects of the nesting cycle. Males actively guard females during nest site selection, and the pair constructs a pensile nest in the fork of a branch over the course of three days (Brown 1993). Females lay one egg per day and four eggs is the modal clutch size of unparasitized nests at our study site (Parker 1999). Both sexes incubate the eggs for ~14 days and provision the brood for ~12 days until the young fledge. Similar to other vireo species, adult Bell's Vireos provide extensive post-fledging care and the family group may remain in the vicinity of the territory for >30 days after the young leave the nest. Although vireos frequently renested following nest failure, pairs raised a maximum of one brood per year at our study site (K. L. Kosciuch, *unpublished data*).

We monitored nests every three days and considered a nest "parasitized" if it contained at least one cowbird egg and "unparasitized" if it contained only host eggs. Nests that were abandoned during nest building were discarded from analysis ($n = 14$). Vireo eggs are white with sparse pink spotting and were easily distinguished from the larger cowbird eggs with brown speckling (see Plate 1). We determined that cowbird eggs were "accepted" if the vireo pair initiated incubation of a parasitized clutch. Thus, cowbird eggs may have been in the nest between one and 5 days before we considered them accepted. Studies of host responses to experimental parasitism often use a criterion of five days to determine acceptance or rejection of parasitic eggs (e.g., Davis et al. 2002, Peer et al. 2002). However, some researchers suggest that host response within 24 hours provides more information regarding host behavior (Rothstein 1982, Peer and Sealy 2004). We found that no parasitized nests were deserted after the pair began incubating if there was no change in clutch size. Further, cowbird eggs were accepted at all nests when parasitism

occurred during incubation (1% of nests, $n = 392$). Nests were “multiple parasitized” if two or more cowbird eggs were found in a nest. If the eggs were cold and the nest was left unattended for at least three days, we considered the nest to be “deserted.” If the entire contents of the nest disappeared during incubation or brooding, we considered the nest to be “depredated.” Similarly, if a nest was empty prior to the expected fledging date and the pair attempted a new nest within the territory, we assumed that the previous nest was depredated. We considered nests to be “successful” if at least one vireo or cowbird fledgling was produced. We confirmed fledging by locating scolding adults and family groups after young had departed from the nest.

Statistical analysis

The effects of cowbird removal on parasitism and nest desertion by vireos.—To test for initial plot differences, we used data from 2003 to examine patterns of parasitism and nest desertion among our four study plots. Data were pooled within treatments for subsequent analyses because the probabilities of parasitism and nest desertion did not differ among plots within treatments (see *Results*). To test our hypotheses regarding the effects of cowbird removal, we limited our analyses to data from 2004 and 2005 when removals were conducted.

To model the probabilities of parasitism and desertion of parasitized nests, we used logistic regression in SAS software (Version 9.1, PROC GENMOD). A set of a priori candidate models, which contained factors we believed to be relevant, were developed prior to analysis. Candidate models for the probabilities of parasitism and the probability of nest desertion contained three factors: treatment (unmanipulated or cowbird removal), year (2004 or 2005 to control for annual variation in parasitism), and week of clutch initiation (to control for seasonal declines in parasitism). We set week 1 = 9–15 May. We used the Hosmer-Lemeshow test to examine goodness of fit of the fully parameterized (global) model and concluded that the model was a good fit to the data if we did not reject the null hypothesis. We examined the β estimates to determine the direction of the effect, and exponentiated β (e^β) to obtain the odds ratio. Odds ratios >1 indicate that the factor increased the odds of an event, whereas odds ratios <1 indicate the opposite. Model selection was based on Akaike Information Criterion values corrected for small sample size (AIC_c). If nested models differed by only one parameter and $\Delta AIC_c \leq 2$, we based model selection on changes in model deviance instead (Guthery et al. 2005). Ratios of Akaike weights (w_i) were used to determine the degree of support for a candidate model.

We used general linear models (PROC GLM) to examine the effects of treatment and season on the number of cowbird eggs per parasitized nest. Parasitism intensity is often correlated with parasitism frequency and other metrics of productivity (Jensen and Cully

2005). Therefore, we included only the factors from the top logistic regression model for the probability of parasitism in all subsequent analyses. Although count data such as the number of eggs or fledglings per nest may not be normally distributed, the F test is robust against departures from normality and heterogeneity of variances when sample sizes are large and values are skewed in the same direction (Lindman 1974). Our starting model contained treatment and week, and we eliminated terms from the model when P values for type III sums of squares were >0.05 .

The effects of cowbird removal on host and parasite productivity.—We used data from 2004 and 2005 to model productivity per nest and seasonal fecundity. Seasonal fecundity is a more informative metric because productivity per nest fails to account for variation in number of nesting attempts (Pease and Grzybowski 1995, Grzybowski and Pease 2005). We report both metrics because past studies of unmarked birds have reported productivity per nest. To examine how cowbird removal and parasitism affect vireo and cowbird productivity, we first tested for differences in the mean number of vireo eggs per nest between treatments. To determine how cowbird removals influenced the probability of nest success, we used a logistic regression model, and included the factors treatment and parasitism status. We did not use Mayfield estimators or nest survival models in Program MARK because nests were usually found during nest construction. Although vireos usually fail to fledge young from parasitized nests, we considered nests that fledged only cowbirds to be successful because the nest escaped predation and produced young. Egg removal by cowbirds during the vireo laying cycle can cause nest desertion (Kosciuch et al. 2006), but we were interested in losses to predation past the primary stage of cowbird activity. To determine if the probability of failure of parasitized nests was higher at unmanipulated plots than removal plots, we used logistic regression and limited our analysis to parasitized nests that survived the egg laying stage. Last, we used a mixed model (PROC MIXED), with pair nested within treatment as a random effect and modeled vireo productivity per pair to determine if the mean number of vireo or cowbird fledglings per pair differed between treatments.

Effect size estimates.—To determine the magnitude of the effect of cowbird removal on productivity of vireos and cowbirds from vireo pairs, we calculated an effect size (Hedge's d) across unmanipulated and removal plots for each year (Gurevitch and Hedges 1999). To examine interspecific variation in the effects of cowbird removal on host and parasite productivity, we also calculated effect sizes for published estimates of host and cowbird productivity for Song Sparrows (Smith et al. 2002).

RESULTS

Cowbird removals

We captured and removed a similar number of female cowbirds in each year at all removal plots combined

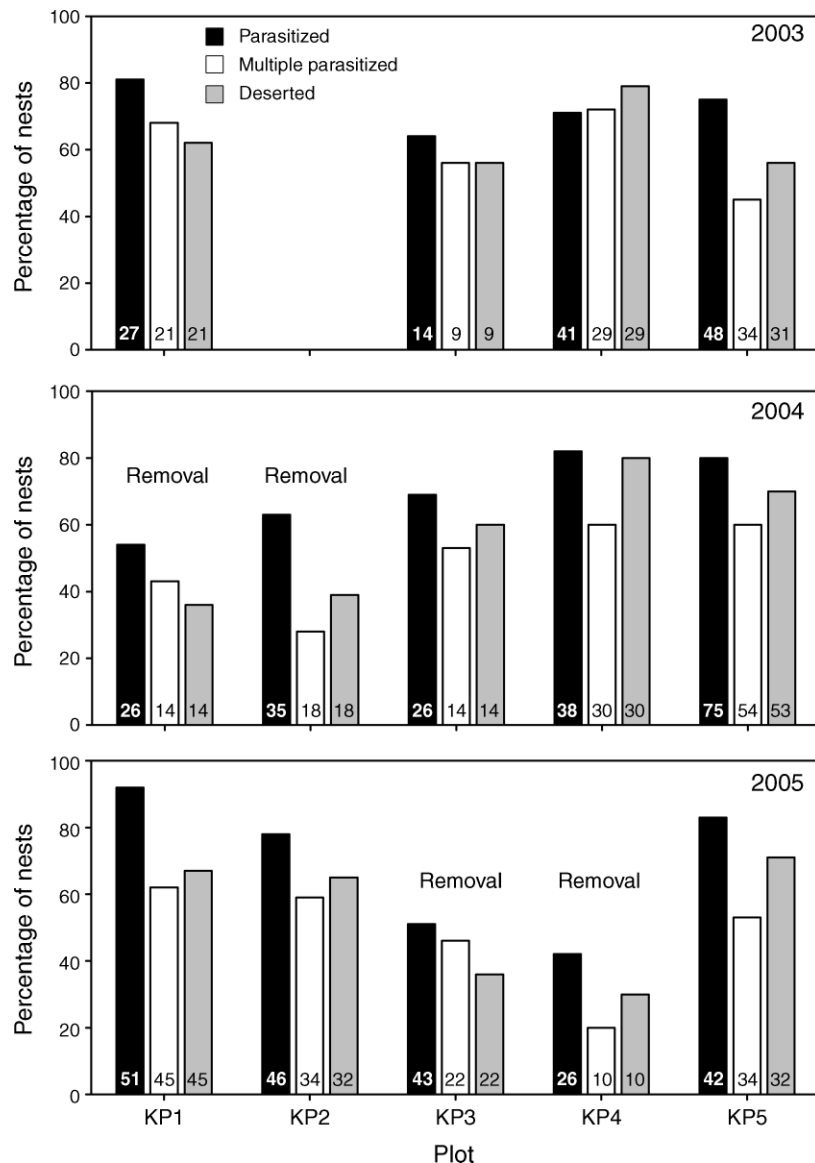


FIG. 1. Percentage of Bell's Vireo nests parasitized (solid bars), multiple parasitized (>1 cowbird egg per parasitized nest, open bars), and deserted (gray bars) at cowbird removal and unmanipulated plots at Konza Prairie Biological Station, Kansas, 2003–2005. Plots are unmanipulated unless labeled “removal”; sample size is in the bar. Plot KP2 was not used in 2003.

(2004, $n = 76$; 2005, $n = 95$). However, we captured approximately twice as many males in 2005 ($n = 493$) compared to 2004 ($n = 231$). The number of juveniles captured was similar in both years (2004, $n = 39$; 2005, $n = 46$).

The effects of cowbird removal on parasitism and nest desertion

We located 538 nests that could be classified as parasitized or unparasitized. Ninety-one percent of nests were located during nest building or egg-laying, 8% were found during incubation, and only 1% were located during brood-rearing. We were able to assess vireo response (accept or desert) for 94% of the parasitized

nests ($n = 392$). In 2003, our observational year, parasitism frequency ranged from 64% to 81% per plot (overall mean = $74\% \pm 0.6\%$ SE, $n = 130$), and did not differ among plots ($\chi^2 = 1.71$, $df = 3$, $P = 0.63$, Fig. 1). We pooled plots within treatments for subsequent analyses.

Experimental cowbird removals reduced parasitism frequency in both removal years from an average of $77\% \pm 0.6\%$ (mean \pm SE, $n = 139$) at unmanipulated plots to $58\% \pm 0.8\%$ ($n = 61$) at cowbird removal plots in 2004, and from an average of $85\% \pm 0.6\%$ ($n = 139$) at unmanipulated plots to $47\% \pm 0.8\%$ ($n = 69$) at cowbird removal plots in 2005 (Fig. 1). We did not find a carryover effect of cowbird removal on parasitism

TABLE 1. Logistic regression model results for the probability of parasitism and desertion of parasitized Bell's Vireo nests at Konza Prairie Biological Station, Kansas, USA.

Model factors	<i>K</i>	Deviance	AIC _c	ΔAIC _c	<i>w_i</i>
Probability of parasitism					
Week, treatment	3	412.7	418.7	0.0	0.56
Year, week, treatment	4	411.4	419.5	0.8	0.37
Year, week, treatment, plot	8	407.7	424.1	5.4	0.04
Global	9	407.2	425.7	6.4	0.02
Probability of nest desertion					
Week, treatment	3	329.2	335.3	0.0	0.48
Treatment	2	332.8	336.9	1.6	0.22
Year, week, treatment	4	329.2	337.3	2.0	0.18
Year, treatment	3	332.6	338.7	3.4	0.09
Year, treatment, year × treatment	4	332.6	340.7	5.4	0.03

Notes: ΔAIC_c is the difference between the Akaike Information Criterion value of the best-fitting model (ΔAIC_c = 0) and the additional models; *K* is the number of parameters; *w_i* is the Akaike weight. The global model is year, week, treatment plot, year × treatment. Only models with a *w_i* > 0.01 are shown.

frequency when we compared KP1 ($\chi^2 = 1.72$, *df* = 1, *P* = 0.19) and KP2 ($\chi^2 = 0.36$, *df* = 1, *P* = 0.55) to KP5 in 2005, suggesting that both plots experienced parasitism frequencies similar to unmanipulated plots within a year after cowbird trapping was discontinued.

Our global model for the probability of parasitism was a good fit to the data ($\chi^2 = 10.3$, *df* = 8, *P* = 0.25). The top two models in our candidate set received 93% of the support (Table 1). The top model contained the variables week of clutch initiation and treatment and garnered 56% of the support among the candidate models. A model that contained the factor year had a ΔAIC_c value <2, but the inclusion of year led to only a 0.3% decrease in the model deviance. Thus, we used the minimum AIC_c model to estimate parameters, and the logistic regression equation was

$$\text{Logit}(p) = 2.33 - 0.81(\text{treatment}) - 0.33(\text{week}).$$

The odds of parasitism at unmanipulated plots were 5.0 times greater (CL: 3.0, 8.3, all values are model estimates and 95% CL) than the odds of parasitism at removal plots. The odds of parasitism decreased 28% per week over the course of the breeding season. The probability of parasitism in week 1 at a removal plot (0.77; CL: 0.66, 0.85) was similar to the probability of parasitism in week 6 at an unmanipulated plot (0.77; CL: 0.71, 0.82; Fig. 2A).

Parasitism frequency was positively correlated with the number of cowbird eggs received per vireo nest (*r* = 0.73, *P* = 0.003, *n* = 14), and lower rates of multiple parasitism were found at removal plots (2004, 35% ± 2%, mean ± SE; 2005, 33% ± 1%) than unmanipulated plots (2004, 58% ± 0.4%; 2005, 58% ± 1%; Fig. 1). Week and treatment explained significant variation in the mean number of cowbird eggs per parasitized nest. Parasitized nests at unmanipulated plots contained 0.28 more cowbird eggs per nest on average than parasitized nests at cowbird removal plots ($F_{1,268} = 9.4$, *P* < 0.001; Table 2). The mean number of cowbird eggs per parasitized nest decreased by ~0.06 cowbird eggs per

nest per week throughout the season ($F_{1,268} = 7.9$, *P* = 0.005).

Frequency of desertion among parasitized nests was positively correlated with parasitism frequency (*r* = 0.84, *P* < 0.001, *n* = 14), and lower rates of nest desertion were found at cowbird removal plots (35% ± 0.5%, mean ± SE) compared to unmanipulated plots (69% ± 0.5%;

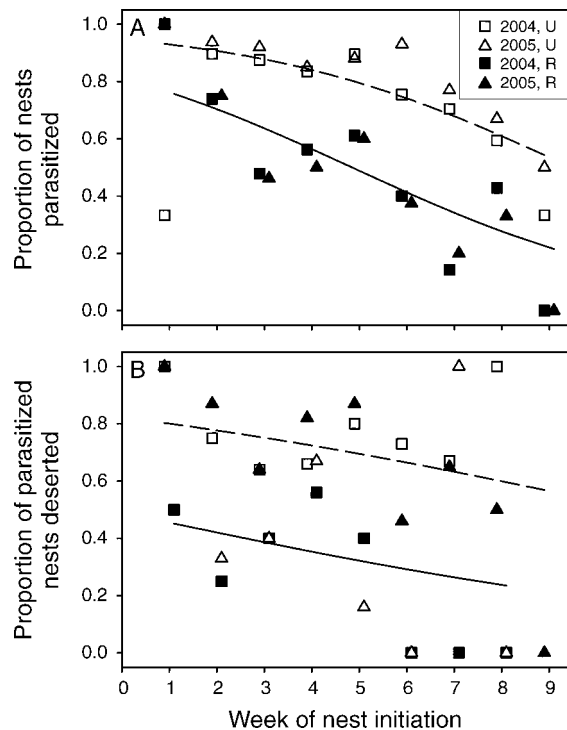


FIG. 2. (A) Proportion of Bell's Vireo nests parasitized, and (B) proportion of parasitized Bell's Vireo nests deserted by week at unmanipulated and Brown-headed Cowbird removal plots in Kansas. The logistic regression lines are fit by treatment with years pooled for each analysis. The solid line is for the unmanipulated treatment, and the dashed line is for the cowbird removal treatment in each graph. Week 1 = 9–16 May.

TABLE 2. Productivity estimates for Bell's Vireos and Brown-headed Cowbirds from unmanipulated (U) plots and cowbird removal (R) plots at Konza Prairie Biological Station, Kansas.

Year	Trt	No. eggs per nest			No. fledglings per egg		
		Vireo eggs per unparasitized nest	Vireo eggs per parasitized nest	Cowbird eggs per parasitized nest	Vireo, from unparasitized nests	Vireo, from parasitized nests	Cowbird, from parasitized nest
2003	U	3.48 ± 0.16 (33)	1.62 ± 0.15 (94)	1.68 ± 0.07 (96)	0.62 (115)	0.005 (213)	0.09 (160)
2004	U	3.30 ± 0.17 (30)	1.51 ± 0.13 (109)	1.64 ± 0.07 (109)	0.46 (98)	0.03 (182)	0.03 (179)
2005	U	3.47 ± 0.16 (21)	1.27 ± 0.14 (113)	1.67 ± 0.07 (118)	0.48 (73)	0 (223)	0.02 (197)
Pooled	U	3.42 ± 0.09 (84)	1.65 ± 0.07 (316)	1.66 ± 0.04 (323)	0.53 (286)	0.01 (618)	0.04 (536)
2004	R	3.76 ± 0.12 (25)	2.22 ± 0.25 (36)	1.39 ± 0.10 (36)	0.68 (94)	0.05 (88)	0.16 (50)
2005	R	3.83 ± 0.10 (35)	2.40 ± 0.18 (32)	1.36 ± 0.09 (33)	0.49 (134)	0 (77)	0.14 (44)
Pooled	R	3.80 ± 0.07 (60)	2.31 ± 0.16 (68)	1.38 ± 0.07 (69)	0.57 (228)	0.03 (165)	0.15 (94)

Notes: "Trt" refers to treatment. Values for eggs per nest are means ± SE. Sample sizes (*n*) are in parentheses: for eggs per nest, *n* is total number of nests; for fledglings per egg, *n* is total number of eggs pooled within a treatment year.

Fig. 1). Our global model for the probability of nest desertion was a good fit to the data ($\chi^2 = 1.97$, $df = 8$, $P = 0.98$). The top model contained treatment and week of clutch initiation, and garnered 48% of the support among the set (Table 1). The second best model contained treatment alone and received 22% of the support among the candidate set. Although two models had a ΔAIC_c value <2, we derived parameter estimates from our minimum AIC_c model because it received 2.2 times the support of the next best model. The logistic regression equation for the top model was

$$\text{Logit}(p) = 0.49 - 0.80(\text{treatment}) - 0.14(\text{week}).$$

The odds of desertion at unmanipulated plots were 4.9 times (CL: 2.7, 9.1) greater than the odds of desertion at removal plots. The odds of desertion decreased 13% per week over the course of the breeding season. The probability of desertion in week 1 at a removal plot (0.45; CL: 0.30, 0.61) was lower than the probability of desertion in week 9 at an unmanipulated plot (0.57; CL: 0.39, 0.72; Fig. 2B).

The effects of parasitism and cowbird removal on host and parasite productivity

The mean number of vireo eggs in unparasitized nests showed little variability between treatments, regardless of year, and averaged 3.3–3.8 eggs per plot (Table 2). In contrast, the mean number of vireo eggs in parasitized nests was ~0.7–1.1 eggs greater at removal plots in 2004 and 2005 (Table 2). A model that contained treatment, week, and parasitism status explained significant variability in the number of vireo eggs per nest ($F_{3,376} = 77.6$, $P < 0.001$). Although vireo clutch size did not decline seasonally ($F_{1,376} = 1.3$, $P = 0.25$), mean number of vireo eggs per nest differed between treatments ($F_{1,376} = 27.6$, $P < 0.001$), and between parasitized and unparasitized nests ($F_{1,376} = 130.4$, $P < 0.001$; Table 2).

We found a significant interaction between treatment and parasitism status for the probability of nest success when we used data from all nests ($\chi^2 = 5.36$, $df = 1$, $P = 0.02$). Unparasitized nests (unmanipulated, probability of success = 0.51, CL: 0.38, 0.64; cowbird removal, probability of success = 0.63, CL: 0.50, 0.73), had a

higher probability of success than parasitized nests (unmanipulated, probability of success = 0.05, CL: 0.03, 0.06; cowbird removal, probability of success = 0.23, CL: 0.18, 0.35). Controlling for parasitism status, the odds of success at cowbird removal plots was 3.1 times (CL: 1.7, 5.4) greater than the odds of success at unmanipulated plots. Controlling for treatment, the odds of success of an unparasitized nest was 10.6 times (CL: 6.0, 18.5) greater than the odds of success for a parasitized nest. When we limited our analysis to nests that survived the vireo egg-laying stage, treatment ($\chi^2 = 7.3$, $df = 1$, $P = 0.007$) and parasitism status ($\chi^2 = 27.7$, $df = 1$, $P < 0.001$) explained significant variation in the probability of success. Nests at cowbird removal plots had a higher probability of success (unparasitized, probability of success = 0.67, CL: 0.56, 0.76; parasitized, probability of success = 0.31, CL: 0.21, 0.43), compared to nests at unmanipulated plots (unparasitized: probability of success = 0.48, CL: 0.36, 0.60; parasitized: probability of success = 0.17, CL: 0.11, 0.25). For both treatments combined, parasitized nests were more likely to fail during the incubation stage than during the brood rearing stage ($\chi^2 = 8.8$, $df = 1$, $P = 0.002$, $n = 131$).

Vireo productivity was higher at cowbird removal plots (1.1 ± 0.1 vireo fledglings/nest, mean ± SE) than at unmanipulated plots (0.4 ± 0.05 vireo fledglings/nest; $F_{1,406} = 34.7$, $P < 0.001$; Fig. 3A). Unexpectedly, productivity of cowbird young from vireo nests was also higher at removal plots (0.1 ± 0.03 young/nest, mean ± SE) than at unmanipulated plots (0.06 ± 0.01 ; $F_{1,406} = 12.8$, $P < 0.001$; Fig. 3B). We found no evidence of carryover effects on the number of vireo fledglings per nest for KP1 (2004 removal year, 1.27 ± 0.33 vireo fledglings/nest, mean ± SE, $n = 26$; 2005 unmanipulated year, 0.12 ± 0.09 vireo fledglings/nest, $n = 51$), or for KP2 (2004 removal year, 1.03 ± 0.28 vireo fledglings/nest, $n = 35$; 2005 unmanipulated year, 0.46 ± 0.18 vireo fledglings/nest, $n = 46$) when compared to the permanent unmanipulated plot (KP5) in 2005 (0.19 ± 0.11 vireo fledglings/nest, $n = 42$). Thus, vireo productivity per nest returned to pre-removal levels after trapping was suspended.

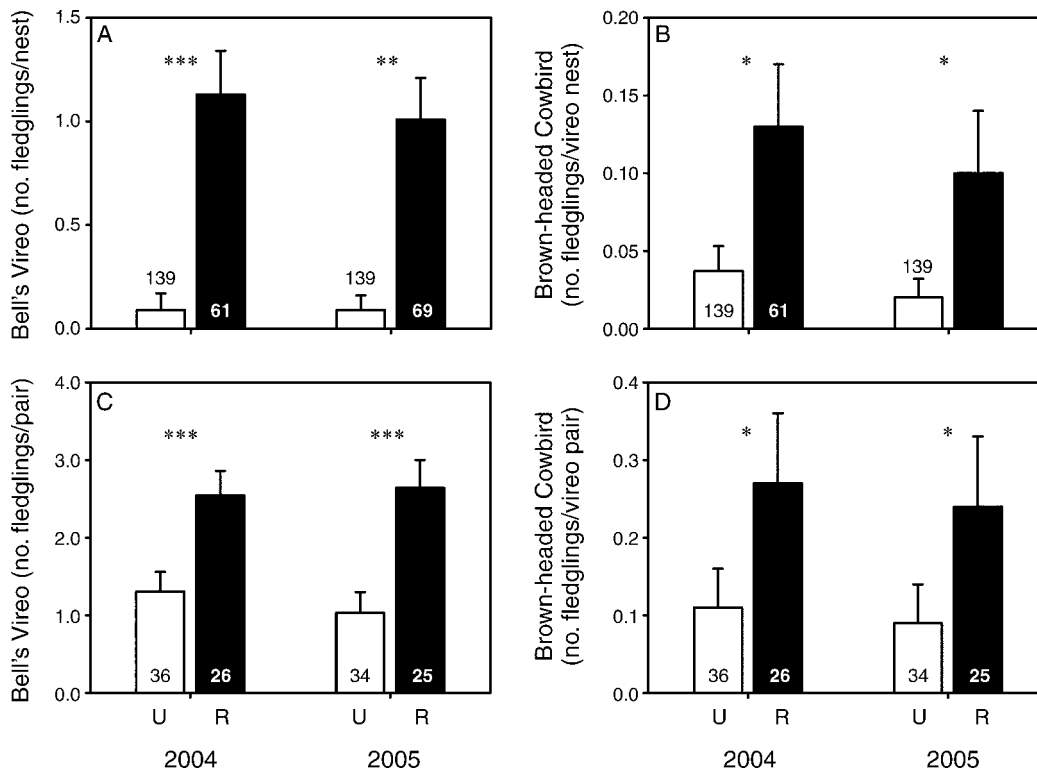


FIG. 3. (A) Bell's Vireo fledglings per nest (mean + SE), (B) Brown-headed Cowbird fledglings per Bell's Vireo nest (mean + SE), (C) Bell's Vireo fledglings per vireo pair (mean + SE), and (D) Brown-headed Cowbird fledglings per vireo pair (mean + SE) at unmanipulated plots (U; open bars) and Brown-headed Cowbird removal plots (R; solid bars) in Kansas. Results from ANOVA and mixed model: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The number of vireo fledglings produced per vireo egg in unparasitized nests was similar at cowbird removal plots (0.57 , $n = 228$ eggs pooled across years) and unmanipulated plots (0.53 , $n = 286$; Table 2). Cowbird removals did not influence the number of vireo fledglings produced per vireo egg in parasitized nests, and fledging success was 0.02 ($n = 783$) for both treatments combined. Only 2% (6/392) of parasitized nests fledged vireo young. In three nests the cowbird egg was laid before the vireo nest was complete and was incorporated into the nest lining, in one nest the cowbird egg failed to hatch, and in two nests, the cowbird egg was laid during vireo incubation and each nest produced one vireo and one cowbird fledgling. Cowbird fledglings per egg were higher at cowbird removal plots (0.15 , $n = 94$ eggs pooled across years) compared to unmanipulated plots (0.04 , $n = 536$).

Parasitism frequency explained 93% of the variation in vireo fledglings per pair ($P = 0.009$). Vireo pairs fledged more vireo young at cowbird removal plots (2.6 ± 0.2 vireo fledglings/pair, mean \pm SE) compared to unmanipulated plots (1.2 ± 0.1 vireo fledglings/pair; $F_{1,118} = 22.7$, $P < 0.0001$; Fig. 3C). Vireo pairs fledged more cowbird young at removal plots (0.3 ± 0.06 cowbird fledglings/pair) than at unmanipulated plots

(0.1 ± 0.03 cowbird fledglings/pair; $F_{1,118} = 5.24$, $P < 0.02$; Fig. 3D).

Effect size estimates

Effect sizes of cowbird removals on the seasonal fecundity of hosts were similar for vireos in both years of this study (2004, $d = 0.78 \pm 0.07$ variance; 2005, $d = 0.96 \pm 0.08$) and were comparable to published estimates for Song Sparrows (1997, $d = 0.74 \pm 0.07$; 1998, $d = 1.02 \pm 0.08$; Smith et al. 2002). In contrast, cowbird removals had a positive effect on the productivity of cowbirds from vireo pairs (2004, $d = 0.59 \pm 0.07$; 2005, $d = 0.59 \pm 0.07$), but not from Song Sparrow pairs (1997, $d = -0.43 \pm 0.07$; 1998, $d = -0.36 \pm 0.07$). Thus, cowbird removal consistently increased productivity for two songbird hosts, but our results differed markedly because cowbird removals unexpectedly increased cowbird productivity from vireo nests.

DISCUSSION

The results from our experimental cowbird removals met three of four of our predictions and demonstrate that cowbird parasitism is a factor limiting productivity of Bell's Vireos in Kansas. First, cowbird removals reduced the probability of parasitism and the number of cowbird eggs per parasitized nest, and increased vireo



PLATE 1. Bell's Vireo nest containing three Bell's Vireo eggs and one Brown-headed Cowbird egg at Konza Prairie Biological Station, Kansas, USA. Photo credit: K. Kosciuch.

productivity per nest and per pair. Our results were consistent among years and replicate plots, and removal of cowbird traps had no obvious carryover effects on the probability of parasitism or vireo productivity. Cowbird removals resulted in a 10-fold increase in vireo productivity per nest, but only a twofold increase in seasonal fecundity. Despite the difference in the magnitude of the effects, the pattern was for higher productivity and fecundity of the host at cowbird removal plots. Seasonal declines in parasitism at our study site allowed some renesting pairs to raise an unparasitized brood, but were not sufficient to increase vireo productivity at unmanipulated plots to levels similar to those at cowbird removal plots.

Second, the probability of nest desertion was lower at cowbird removal plots relative to unmanipulated plots, and we attribute the difference to fewer instances of vireo egg loss during the laying stage. Thus, vireos experienced the cue to desert less often when cowbird density was experimentally reduced. Third, the probability of nest success was higher for unparasitized nests than parasitized nests, suggesting that cowbirds may cause nest failure during the incubation or brood rearing stages. Furthermore, the probability of success for parasitized nests was higher at removal plots than at unmanipulated plots, possibly due to reduced cowbird activity. Last, and counter to our prediction, cowbird removals had the undesirable effect of increasing cowbird productivity from vireo nests.

Understanding how parasitism and predation interact to limit host productivity is essential to successful

management of songbird species because cowbird removals may not increase host productivity if nest failure rates are high (Woodworth 1997, 1999). Conversely, cowbird removals may substantially increase host productivity if cowbirds are a nest predator (Arcese et al. 1996, Smith et al. 2002, 2003). In this study, vireo productivity increased primarily due to decreases in parasitism because unparasitized nests had similar probabilities of nest success and produced a similar number of vireo fledglings per egg for both treatments. As a coarse estimate of population growth, we used fecundity (F) estimates from this study, an adult survival rate of $S_a = 0.61$ from a Bell's Vireo population in Missouri (Budnik et al. 2001), and a juvenile survival rate that was assumed to be half of adult survival ($S_j = 0.5S_a$; Fletcher et al. 2006). The estimated finite rate of population growth ($\lambda = FS_j + S_a$) was 0.79 at unmanipulated plots and 1.0 at cowbird removal plots. Thus, without immigration, current levels of cowbird parasitism combined with nest predation at our study site would result in a declining vireo population ($\lambda < 1.0$).

The probability of nest success was lower for parasitized nests than unparasitized nests. This pattern is predicted to emerge at high cowbird densities when female laying ranges overlap, and our results support a key prediction of the cowbird predation hypothesis. At high cowbird densities, nests that escape parasitism during the host laying stage should be less likely to be located by cowbirds at later stages compared to nests that were previously parasitized. Alternatively, parasit-

ized nests may fail at higher rates if begging by cowbird nestlings increases the conspicuousness of the nest to predators (Dearborn 1999, Aviles et al. 2006). However, we found that a larger proportion of parasitized nests failed during the incubation stage when begging by cowbirds would not be a factor. Parasitized nests had a higher probability of success at cowbird removal plots than at unmanipulated plots, suggesting that cowbirds may depredate parasitized nests at our study site. Alternatively, multiple visits by cowbirds may result in increased parental activity in nest defense and result in higher rates of depredation (Martin et al. 2000, Zanette et al. 2007). Regardless of the underlying mechanism, higher parasitism frequencies were associated with lower probabilities of success for parasitized nests. Understanding patterns of predation for parasitized and unparasitized nests is important because large-bodied hosts (e.g., Song Sparrow) can fledge host and parasitic young from mixed broods, and increased survival of parasitized nests could increase cowbird productivity in some host species (Smith et al. 2002).

Cowbird productivity from vireo nests was higher at cowbird removal plots than unmanipulated plots, and a positive effect of cowbird removals on cowbird productivity has not been previously reported. Reduced cowbird density may be of greatest benefit to cowbirds when hosts use cues to desert nests that are correlated with cowbird density, or density of suitable hosts is low relative to cowbird density. Thus, cowbird removals not only affect the productivity of the trapped individuals, removals may also indirectly affect the productivity of free-living cowbirds through density-dependent effects on host behavior and nest success. Although vireos did not fledge multiple cowbird nestlings from a single nest, cowbird removals could increase cowbird productivity from host species capable of raising mixed broods, such as Dickcissel or Wood Thrush (*Hylocichla mustelina*) because hatching and fledging success of cowbird eggs are negatively correlated with parasitism intensity (Trine 2000, Jensen and Cully 2005). Our study demonstrates the importance of understanding the overall effect of cowbird removals on host and cowbird population dynamics. Community-wide studies are needed to determine if decreases in cowbird productivity from one host are offset by increases in cowbird productivity from other hosts within the community.

The effects of parasitism and cowbird removals on the productivity of vireos vary across their breeding range. In California, productivity of the Least Bell's Vireo has increased in areas with cowbird removals, and the vireo populations have increased eightfold (Kus and Whitfield 2005). Although productivity at reference areas was not monitored and the effects of removals are difficult to evaluate, parasitism frequency alone explained 65% of the variability in productivity per pair, suggesting that cowbird parasitism is a limiting factor (Kus and Whitfield 2005). In contrast to our results, the probability of parasitism increased throughout the vireos'

breeding season in California, thus decreasing the likelihood of a vireo pair successfully fledging young as the season progressed (Kus 2002). Cowbird removals had mixed effects on the productivity of Bell's Vireos breeding in Arizona (Morrison and Averill-Murray 2002). Parasitism frequency was lower at their cowbird removal plots, but nest failure rates were high and masked the effect of removals in one study year. Thus, the benefits of cowbird removals may vary regionally for a species because of interactions among seasonal patterns of parasitism and predation.

Small-bodied hosts with long incubation periods typically suffer the highest costs of parasitism (Hauber 2003b). However, based on effect size estimates of seasonal productivity, cowbird removals had a similar effect on productivity of Bell's Vireo (9 g) compared to the larger bodied Song Sparrows (20 g). Bell's Vireos benefited primarily from decreased parasitism frequency (see *Results*), whereas increased Song Sparrow productivity resulted from decreased parasitism frequency and increased survival rate of sparrow nests (Smith et al. 2002). Furthermore, Song Sparrows often fledge host young from parasitized nests, and increased survival rates of parasitized nests would increase sparrow productivity, but not vireo productivity. In a concurrent study of Dickcissels (27 g) at our study site, Sandercock et al. (B. K. Sandercock, E. L. Hewett, and K. L. Kosciuch, *unpublished manuscript*) found no effect of cowbird removal on Dickcissel productivity per nest due to high rates of nest predation. Similarly, cowbird removals did not increase nest success of California Gnatcatchers (*Polioptila californica*, 6 g) because of high predation rates (Braden et al. 1997). Thus, the demographic benefits of cowbird removals may be limited by predation rates, and host body size may not be a reliable indicator of how the species will respond to experimentally decreased parasitism.

Management and conservation implications

It is largely unknown how suspension of cowbird removal programs will affect the productivity and population growth of threatened or endangered songbirds because most management programs do not monitor productivity in unmanipulated reference areas. We found that after cowbird removals were discontinued, parasitism frequency and vireo productivity returned to pre-trapping levels quickly, possibly because cowbirds emigrated from surrounding areas. Similarly, Smith et al. (2002) found that parasitism increased and productivity of Song Sparrows decreased following the removal of cowbird traps when parasitism frequencies at control areas were moderate (53–66% of nests parasitized). If the number of female cowbirds captured at the hosts' breeding area is an indicator of parasitism potential, then our results suggest that parasitism frequency might return to baseline levels if long-term trapping is suspended in areas of ongoing cowbird control, especially where parasitism frequencies are

moderate to high at control areas (e.g., DeCapita 2000, Kostecke et al. 2005). Thus, any planned decreases in cowbird trapping effort should consider how recent trends in cowbird density or capture rate may influence parasitism and host productivity.

Managers should consider the short and long-term trade-offs between changes in host and cowbird productivity, especially in areas of high cowbird density. In our study, both host (2.2 times higher at removal plots) and cowbird (3.0 times higher at removal plots) productivity per host pair increased. Despite a threefold increase in cowbird productivity, only three in 10 vireo pairs, on average, produced a cowbird young at removal plots. Thus, the biological benefits of cowbird removals are likely greater for vireos than cowbirds. In the future, better demographic data on the egg-laying behavior of individual female cowbirds, and estimates of host and parasite survival rates will be necessary to determine whether host-specific changes in cowbird productivity would have short or long-term effects on host populations in songbird communities.

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LITERATURE CITED

- Arcese, P., J. N. M. Smith, and M. I. Hatch. 1996. Nest predation by cowbirds and its consequences for passerine demography. *Proceedings of the National Academy of Sciences (USA)* 93:4608–4611.
- Aviles, J. M., B. G. Stokke, and D. Parejo. 2006. Relationship between nest predation suffered by hosts and Brown-headed Cowbird parasitism: a comparative study. *Evolutionary Ecology* 20:97–111.
- Braden, G. T., R. L. McKernan, and S. M. Powell. 1997. Effects of nest parasitism by the Brown-headed Cowbird on nesting success of the California Gnatcatcher. *Condor* 99: 858–865.
- Briggs, J. M., A. K. Knapp, J. M. Blair, J. A. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition. Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243–254.
- Briggs, J. M., A. K. Knapp, and B. L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *American Midland Naturalist* 147:287–294.
- Brown, B. T. 1993. Bell's Vireo (*Vireo bellii*). Pages 1–20 in F. Gill and A. Poole, editors. *Birds of North America*, Number 35. American Ornithologists' Union, Washington, D.C., USA.
- Budnik, J. M., D. E. Burhans, M. R. Ryan, and F. R. Thompson. 2001. Nest desertion and apparent nest protection behavior by Bell's Vireos in response to cowbird parasitism. *Condor* 103:639–643.
- Budnik, J. M., M. R. Ryan, and F. R. Thompson. 2000. Demography of Bell's Vireos in Missouri grassland-shrub habitats. *Auk* 117:925–935.
- Davies, N. B. 2000. *Cuckoos, cowbirds and other cheats*. Princeton University Press, Princeton, New Jersey, USA.
- Davies, N. B., and M. D. Brooke. 1989. An experimental study of co-evolution between the Cuckoo, *Cuculus-canorus*, and its hosts. 1. Host egg discrimination. *Journal of Animal Ecology* 58:207–224.
- Davis, S. K., D. R. Klippenstine, and R. M. Brigham. 2002. Does egg rejection account for the low incidence of cowbird parasitism in Chestnut-collared Longspurs (*Calcarius ornatus*)? *Auk* 119:556–560.
- Dearborn, D. C. 1999. Brown-headed Cowbird nestling vocalizations and risk of nest predation. *Auk* 116:448–457.
- DeCapita, M. E. 2000. Brown-headed Cowbird control on Kirtland's Warbler nesting areas in Michigan. Pages 333–341 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin, Texas, USA.
- Fletcher, R. J., Jr., R. R. Koford, and D. A. Seaman. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management* 70:145–157.
- Friedmann, H. 1955. The honeyguides. *U.S. National Museum Bulletin* 208:1–292.
- Granfors, D. A., P. J. Pietz, and L. A. Joyal. 2001. Frequency of egg and nestling destruction by female Brown-headed Cowbirds at grassland nests. *Auk* 188:765–769.
- Griffith, J. T., and J. C. Griffith. 2000. Cowbird control and the endangered Least Bell's Vireo: a management success story. Pages 342–356 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds and their hosts*. University of Texas Press, Austin, Texas, USA.
- Grzybowski, J. A., and C. M. Pease. 2005. Renesting determines seasonal fecundity in songbirds: what do we know? What should we assume? *Auk* 122:280–292.
- Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. *Ecology* 80:1142–1149.
- Guthery, F. S., L. A. Brennan, M. J. Peterson, and J. J. Lusk. 2005. Information theory in wildlife science: critique and viewpoint. *Journal of Wildlife Management* 69:457–465.
- Hartnett, D. C., K. R. Hickman, and L. E. F. Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49:413–420.
- Hauber, M. E. 2003a. Egg-capping is a cost paid by hosts of interspecific brood parasites. *Auk* 120:860–865.
- Hauber, M. E. 2003b. Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. *Behavioral Ecology* 14:227–235.
- Hoover, J. P. 2003. Multiple effects of brood parasitism reduce the reproductive success of Prothonotary Warblers, *Protonotaria citrea*. *Animal Behaviour* 65:923–934.
- Hoover, J. P., and S. K. Robinson. 2007. Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. *Proceedings of the National Academy of Sciences (USA)* 104:4479–4483.
- Jensen, W. E., and J. F. Cully, Jr. 2005. Geographic variation in Brown-headed Cowbird (*Molothrus ater*) parasitism on

- Dickcissels (*Spiza americana*) in great plains tallgrass prairie. *Auk* 122:648–660.
- Kilner, R. M., J. R. Madden, and M. E. Hauber. 2004. Brood parasitic cowbird nestlings use host young to procure resources. *Science* 305:877–879.
- Kosciuch, K. L. 2006. Host-parasite interactions on an experimental landscape. Dissertation. Kansas State University, Manhattan, Kansas, USA.
- Kosciuch, K. L., T. H. Parker, and B. K. Sandercock. 2006. Nest desertion by a cowbird host: anti-parasite behavior or a response to egg loss? *Behavioral Ecology* 17:917–924.
- Kostecke, R. M., S. G. Summers, G. H. Eckrich, and D. A. Cimprich. 2005. Effect of Brown-headed Cowbird (*Molothrus ater*) removal on Black-capped Vireo (*Vireo atricapilla*) nest success and population growth at Fort Hood, Texas. Pages 28–37 in C. P. Ortega, J. F. Chace, and B. D. Peer, editors. Management of cowbirds and their hosts: balancing science, ethics, and mandates. Ornithological Monographs Number 57. American Ornithologists' Union, Washington, D.C., USA.
- Kus, B. E. 2002. Fitness consequences of nest desertion in an endangered host, the Least Bell's Vireo. *Condor* 104:795–802.
- Kus, B. E., and M. J. Whitfield. 2005. Parasitism, productivity, and population growth: response of Least Bell's Vireo (*Vireo bellii pusillus*) and Southwestern Willow Flycatcher (*Empidonax traillii eximius*) to cowbird (*Molothrus* spp.) control. Pages 16–27 in C. P. Ortega, J. F. Chace, and B. D. Peer, editors. Management of cowbirds and their hosts: balancing science, ethics, and mandates. Ornithological Monographs Number 57. American Ornithologists' Union, Washington, D.C., USA.
- Lichtenstein, G., and S. G. Sealy. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic Brown-headed Cowbird chicks in Yellow Warbler nests. *Proceedings of the Royal Society B* 265:249–254.
- Lindman, H. R. 1974. Analysis of variance in complex experimental designs. H. W. Freeman, San Francisco, California, USA.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society B* 267:2287–2293.
- McLaren, C. M., and S. G. Sealy. 2000. Are nest predation and brood parasitism correlated in Yellow Warblers? A test of the cowbird predation hypothesis. *Auk* 117:1056–1060.
- Morrison, M. L., and A. Averill-Murray. 2002. Evaluating the efficacy of manipulating cowbird parasitism on host nesting success. *Southwestern Naturalist* 47:236–243.
- Parker, T. H. 1999. Responses of Bell's Vireos to brood parasitism by the Brown-headed Cowbird in Kansas. *Wilson Bulletin* 111:499–504.
- Pease, C. M., and J. A. Grzybowski. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in songbird birds. *Auk* 112:343–363.
- Peer, B. D. 2006. Egg removal and egg destruction in avian brood parasites. *Auk* 123:16–22.
- Peer, B. D., K. S. Ellison, and S. G. Sealy. 2002. Intermediate frequencies of egg ejection by Northern Mockingbirds sympatric with two cowbird species. *Auk* 119:855–858.
- Peer, B. D., and S. G. Sealy. 2004. Fate of grackle defenses in the absence of brood parasitism: implications for long-term brood parasite–host coevolution. *Auk* 121:1172–1186.
- Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995. Ecology and behavior of cowbirds and their impact on host populations. Pages 428–460 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, London, UK.
- Rothstein, S. I. 1982. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? *Behavioral Ecology and Sociobiology* 11:229–239.
- Rothstein, S. I., and B. D. Peer. 2005. Conservation solutions for threatened and endangered cowbird (*Molothrus* spp.) hosts: separating fact from fiction. Pages 98–114 in C. P. Ortega, J. F. Chace, and B. D. Peer, editors. Management of cowbirds and their hosts: balancing science, ethics, and mandates. Ornithological Monographs Number 57. American Ornithologists' Union, Washington, D.C., USA.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, results and analysis 1966–2004. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. *Condor* 94:40–54.
- Smith, J. N. M., M. J. Taitt, and L. Zanette. 2002. Removing Brown-headed Cowbirds increases seasonal fecundity and population growth in Song Sparrows. *Ecology* 83:3037–3047.
- Smith, J. N. M., M. J. Taitt, L. Zanette, and I. H. Myers-Smith. 2003. How do Brown-headed Cowbirds (*Molothrus ater*) cause nest failures in Song Sparrows (*Melospiza melodia*)? A removal experiment. *Auk* 120:772–783.
- Trine, C. L. 2000. Effects of multiple parasitism on cowbird and Wood Thrush nesting success. Pages 135–144 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, Texas, USA.
- Whitfield, M. J. 2000. Results of a Brown-headed Cowbird control program for the Southwestern Willow Flycatcher. Pages 371–378 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, Texas, USA.
- Woodworth, B. L. 1997. Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. *Condor* 99:605–621.
- Woodworth, B. L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conservation Biology* 13:67–76.
- Zanette, L., D. T. Haydon, J. M. N. Smith, M. J. Taitt, and M. Clinchy. 2007. Reassessing the cowbird threat. *Auk* 124:210–223.